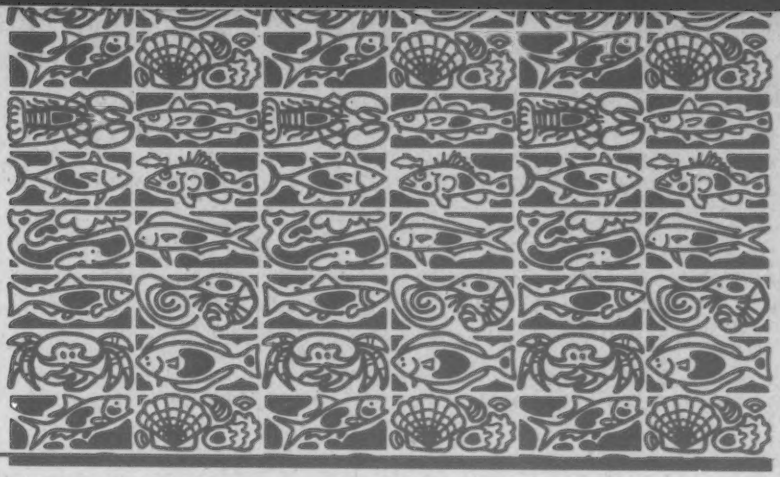

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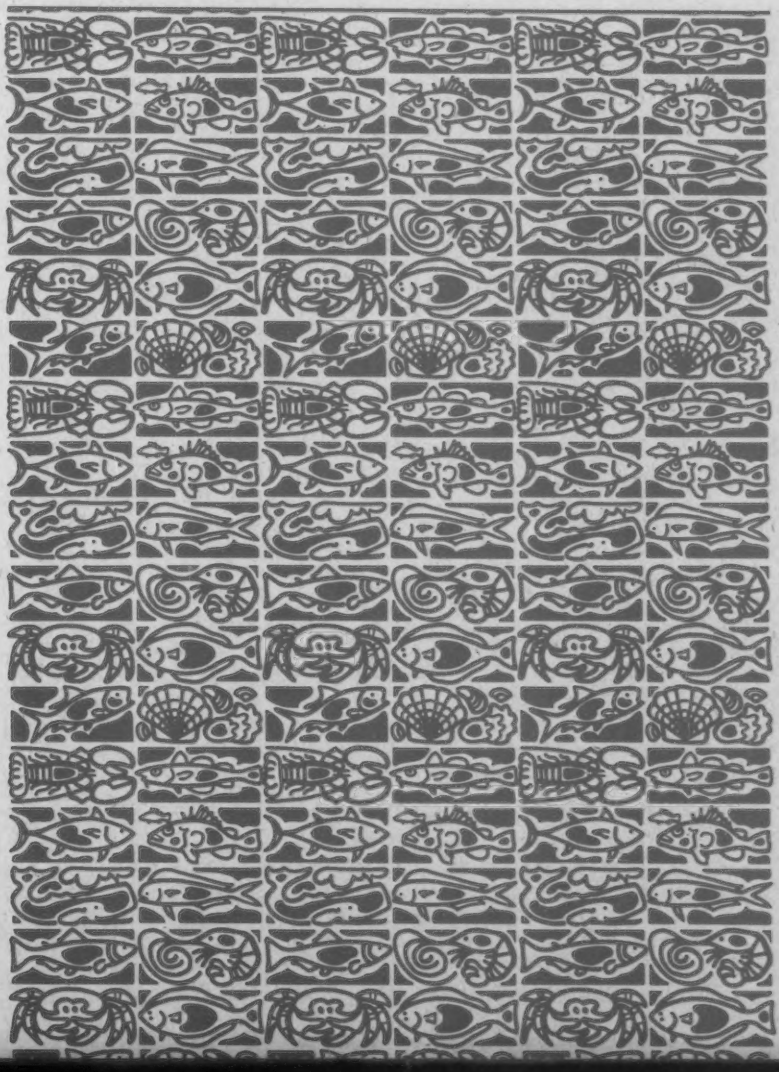

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Yield-per-recruit analysis and management strategies for Atlantic croaker, *Micropogonias undulatus*, in the Middle Atlantic Bight*

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Abstract.—The effect of different fishing mortality (F) and natural mortality (M), and age at first capture (t_c) on yield-per-recruit of Atlantic croaker, *Micropogonias undulatus*, in the lower Chesapeake Bay and North Carolina were evaluated with the Beverton-Holt model. Independent of the level of M (0.20–0.35) or F (0.01–2.0) used in simulations, yield-per-recruit values for Chesapeake Bay were consistently higher at $t_c = 1$ and decreased continuously with increases in t_c (2–5). Although maximum yield-per-recruit always occurred at the maximum level of F (F=2.0), marginal increases in yield beyond F = 0.50–0.75 were negligible. Current F (F_{CUR}) is estimated to be below the level that produces maximum potential yield-per-recruit (F_{MAX}) and at or below the level of $F_{0.1}$ if $M \geq 0.25$. Although modeling results indicated yield-per-recruit could be maximized by reducing the current level of t_c (t_c=2), the resultant gains were small and did not appear to justify such management measures. Instead, it is suggested that regulatory measures be directed at maintaining the current level of t_c in the lower Chesapeake Bay. Simulation results for North Carolina showed a pattern opposite to that shown for Chesapeake Bay, with yield-per-recruit curves increasing consistently with increases in t_c. Estimates of F_{CUR} for $t_c = 1$ were consistently higher than $F_{0.1}$ as well as F_{MAX}, indicating that during the period 1979–81 Atlantic croaker were being growth-overfished in North Carolina. However, differences between Chesapeake Bay and North Carolina seem to reflect temporal rather than spatial differences in Atlantic croaker population dynamics, because data for North Carolina came from a period coinciding with the occurrence of unusually large Atlantic croaker along the east coast of the United States.

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The Atlantic croaker, *Micropogonias undulatus* (Linnaeus), is one of the most important commercial and recreational fishery resources of the southeastern coast of the United States (Wilk, 1981; Schmied and Burgess, 1987; Mercer[1]). Along the Atlantic coast, commercial fisheries for Atlantic croaker are centered in Chesapeake Bay and in North Carolina waters (Joseph, 1972; Rothschild et al., 1981; Ross, 1988; Mercer[1]); both inshore and offshore catches are distributed according to the seasonal migratory patterns of Atlantic croaker. From late spring to early fall Atlantic croaker are caught in estuarine areas, primarily by haul-seine, pound-net, and gill-net fisheries (Ross, 1988; Chittenden, 1991; Barbieri et al., 1994a). From late fall through winter, after adults have moved out of estuaries, they are caught in continental shelf waters by otter-trawl and gill-net fisheries (Wilk, 1981; Ross, 1988; Mercer[1]).

Commercial landings of Atlantic croaker have fluctuated widely over the past 50–60 years (Joseph, 1972; Rothschild et al., 1981; Wilk, 1981). Landings exceeded 20,000 metric tons (t) between 1937 and 1940, peaked at ca. 29,000 t in 1945 and dropped to less than 1,000 t between 1967 and 1971 (Wilk, 1981; McHugh and Conover, 1986). The most recent peak in landings occurred in 1977 and 1978 at just over 13,000 t annually (Mercer[1]). Recreational catches in the mid-Atlantic and South Atlantic regions during 1979–93 have also fluctuated, although they do not reflect fluctuations in commercial landings for the same period. Commercial landings from Virginia and North Carolina—the

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[1] Mercer, L. P. 1987. Fishery management plan for Atlantic croaker (*Micropogonias undulatus*). North Carolina Dep. Nat. Res. Comm. Dev., Div. Mar. Fish., Spec. Sci. Rep. 48, 90 p. [Available from North Carolina Department of Environment, Health, and Natural Resources, Div. Marine Fisheries, PO Box 769, Morehead City, NC 28557-0769.]

two states with 98% of the Atlantic catch—have declined since 1987, whereas recreational catches peaked in 1991 with an estimated 21 million fish (Newlin, 1992; Speir et al., 1994).

A lack of accurate catch and effort data from both the commercial and recreational fisheries makes it difficult to evaluate to what extent these long-term fluctuations represent natural changes in population abundance or reflect historic changes in Atlantic croaker exploitation. There has been a growing concern, however, that recent low landings may be related to the large numbers of young fish killed as bycatch in the southern shrimp fishery and as part of the scrap catch in pound-net, haul-seine, and trawl fisheries (Speir et al., 1994; Mercer[1]). In response to these concerns, the 1993 review of the Atlantic States Marine Fisheries Commission Fishery Management Plan for Atlantic croaker (Speir et al., 1994) has recommended the use of bycatch reduction devices and the establishment of a coast-wide minimum size limit that would maximize Atlantic croaker yield-per-recruit.

Yield-per-recruit models, widely used in fish population dynamics studies (Beverton and Holt, 1957; Ricker, 1975; Gulland, 1983), can be a useful tool in defining routine fisheries management measures such as minimum size limits, closed seasons, etc. (Gulland, 1983; Deriso, 1987). However, the only published application of yield-per-recruit models to Atlantic croaker is based on data from the northwestern Gulf of Mexico (Chittenden, 1977) and points out that results may or may not apply to other areas. In this paper we use stock assessment data from the Chesapeake Bay (years 1988–91; Barbieri et al., 1994a) and from North Carolina (years 1979–81; Ross, 1988) to evaluate the effect of different fishing (-induced) and natural mortality, and age-at-first-capture schedules on Atlantic croaker yield-per-recruit. Implications of this analysis for management of Atlantic croaker are discussed.

Methods

Yield-per-recruit analysis

Yield-per-recruit curves were calculated with the Beverton-Holt yield-per-recruit model (Beverton and Holt, 1957):

$$Y/R = Fe^{-M(t_c - t_r)} W_\infty \sum_{n=0}^{3} \frac{U_n e^{-nK(t_c - t_0)}}{F + M + nK}, \qquad (1)$$

where Y/R = yield-per-recruit in weight (g);

F = instantaneous fishing mortality coefficient;
M = instantaneous natural mortality coefficient;
W_∞ = asymptotic weight (von Bertalanffy growth parameter);
U_n = summation parameter (U_0=1, U_1=–3, U_2=3, U_3=–1);
t_c = mean age at first capture;
t_r = mean age (years) at recruitment to the fishing area;
t_0 = hypothetical age at which fish would have been zero length (von Bertalanffy growth parameter); and
K = the Brody growth coefficient (von Bertalanffy growth parameter).

Computations were performed with the computer program B-H3 available in the Basic Fisheries Science Programs package (Saila et al., 1988).

Parameter values used in simulations are summarized in Table 1. Estimates of growth parameters (W_∞, K, and t_0) for Chesapeake Bay and North Carolina were obtained from Barbieri et al.(1994a) and Ross (1988), respectively. For both areas, W_∞ was converted from L_∞ by using an allometric length-weight relation (b=3.23; Ross, 1988; and b=3.30; Barbieri et al, 1994a). One of the assumptions of the Beverton-Holt yield-per-recruit model is that growth is isometric—i.e. the coefficient b in the length-weight relation is equal to 3 (Beverton and Holt, 1957; Ricker, 1975). We, however, considered that departure from the assumption of isometric growth did not affect interpretation of our modeling results because the factor of interest in these simulations is the relative difference in yield resulting from varying t_c and F at different levels of M. The relative error in such differences, when using an incorrect b, tends to be much less than that in absolute levels (Ricker, 1975).

Estimates of t_r, the mean age at recruitment to the fishing area, were based on Atlantic croaker life history information (Chao and Musick, 1977; Ross, 1988). Estimates of current t_c, the mean age at first capture, was based on Atlantic croaker age compositions reported for the pound-net, haul-seine, and gill-net catches in the lower Chesapeake Bay for the period 1988–91 (t_c=age 2; Barbieri et al., 1994a) and from age compositions reported for the haul-seine fishery in North Carolina for the period 1979–81 (t_c=age 1; Ross, 1988). Because of the uncertainty associated with estimates of M in fish populations (Vetter, 1988), simulations for both areas were conducted over a range of M values (0.20–0.35; Table 1).

The instantaneous total annual mortality rate, Z, for fully recruited Atlantic croaker in North Carolina is 1.3 (Ross, 1988) and ranges from 0.55 to 0.63, with a mean value of 0.59 for the lower Chesapeake

Table 1

Parameter estimates or range of values used in yield-per-recruit simulations for Atlantic croaker, *Micropogonias undulatus*, in the lower Chesapeake Bay (period 1988–91) and North Carolina (period 1979–81). See Equation 1 for definitions of parameter variables.

Parameter	Chesapeake Bay	North Carolina
K	0.36	0.20
W_∞	409.9 g	3,814 g
t_0	–3.26 yr	–0.60 yr
t_r	0 yr	0 yr
t_c	1–5 yr	1–5 yr
F	0.01–2.0	0.01–2.0
M	0.20–0.35	0.20–0.35

Bay (Barbieri et al., 1994a). To estimate current levels of fishing mortality (F_{CUR}) for different values of M, we used $Z = 0.60$ for Chesapeake Bay and $Z = 1.3$ for North Carolina, as

$$F_{CUR} = Z - M_i, \quad (2)$$

where $i = 0.20$, 0.25, 0.30, and 0.35.

The value of $F_{0.1}$ (the level of F for which the marginal increase in yield-per-recruit due to a small increase in F is 10% of the marginal yield-per-recruit in a lightly-exploited fishery [Gulland and Boerema, 1973; Anthony[2]]), was estimated for Chesapeake Bay with $F = 0.01$ and $t_c = 2$ (Barbieri et al., 1994a) and for North Carolina with $F = 0.01$ and $t_c = 1$ (Ross, 1988).

Cohort biomass and harvesting time

In general, the maximum possible yield for a given year class occurs at the critical age t_{CRITIC}, the age where biomass of a cohort is maximum in the absence of fishing. For comparison with the Beverton-Holt yield-per-recruit modeling results, we estimated t_{CRITIC} for Atlantic croaker following Alverson and Carney (1975) and Deriso (1987) as

$$t_{CRITIC} = t_0 + \frac{1}{K}\ln(3K/M + 1), \quad (3)$$

where t_0, K, and M are defined as in Equation 1. Parameter estimates or the range of values used in calculations are listed in Table 1.

[2] Anthony, V. 1982. The calculation of $F_{0.1}$: a plea for standardization. Northwest Atlantic Fisheries Organization, SCR Doc. 82/VI/64 Ser. No. N557, 15 p. NAFO, PO Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

To evaluate the proportion of the potential growth span (P_g) remaining when Atlantic croaker enter the exploited phase of life (Beverton and Holt, 1957), we used the quantity (Beverton, 1963):

$$P_g = (1 - l_c / L_\infty), \quad (4)$$

where L_∞, the asymptotic length, was obtained from Barbieri et al. (1994a) and Ross (1988) and l_c, the average length at first capture, was obtained by converting t_c to length with the von Bertalanffy growth curve reported for Atlantic croaker in Chesapeake Bay (Barbieri et al., 1994a) and North Carolina (Ross, 1988). Both parameters are based on total length (TL) in mm.

Results

Chesapeake Bay

Curves of yield-per-recruit on F (Fig. 1) showed that the yield of Atlantic croaker in Chesapeake Bay could be maximized by decreasing the current level of $t_c = 2$ (265 mm TL) to $t_c = 1$ (245 mm TL). Independent of the level of M or F used in simulations, yield-per-recruit values were consistently higher at $t_c = 1$ and decreased continuously with increasing t_c. However, increases in yield from $t_c = 2$ to $t_c = 1$ were generally small and gradually increased with increases in M. For example, at the estimated current levels of fishing mortality for Atlantic croaker in the Chesapeake Bay (F_{CUR}), increases in yield between $t_c = 2$ and $t_c = 1$ would be 7.1% at $M = 2.0$, 12.6% at $M = 0.25$, 18.4% at $M = 0.30$, and 24.6% at $M = 0.35$.

The curves of yield-per-recruit for Atlantic croaker on F for different levels of M and t_c showed no clearly defined peaks. Although the magnitude of yield curves was dependent on the level of M used in simulations, relative changes in yield as a function of F and t_c were very similar, regardless of M (Fig. 1). For all levels of M and t_c, yield curves increased rapidly in the range of F between 0 and 0.50–0.75, and remained relatively flat thereafter. Although yield values increased continuously with F, i.e. maximum yield-per-recruit always occurred at the maximum value of F used in simulations (F=2.0), increases in yield beyond $F = 0.50$–0.75 were very small. For example, increases in yield from $F = 0.75$ to F_{MAX} ranged from 5.3% to 22.7%, depending on the level of M and t_c used in the model (Table 2). However, this relatively small gain in yield corresponds to an increase in F of 166.7%.

For the range of M used in our study, estimates of F_{CUR} are below the levels that give maximum potential yield-per-recruit (F_{MAX}) and, for $M \geq 0.3$, below

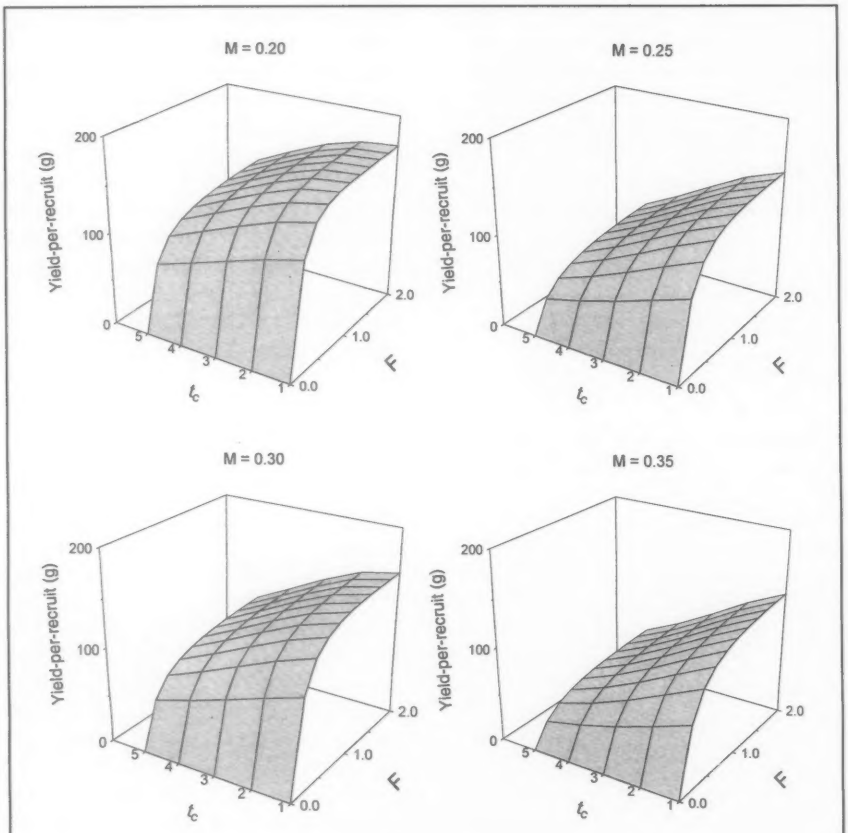

Figure 1

Curves of yield-per-recruit on fishing mortality (F) for Atlantic croaker, *Micropogonias undulatus*, in the lower Chesapeake Bay (period 1988–91) estimated for mean age-at-first-capture (t_c) = 1–5 and natural mortality (M) = 0.20–0.35.

Table 2

Percent increase in yield-per-recruit of Atlantic croaker, *Micropogonias undulatus*, from fishing mortality (F) = 0.75 to fishing mortality at the level that gives maximum potential yield-per-recruit (F_{MAX}) for mean age-at-first-capture (t_c) = 1–5 and natural mortality (M) = 0.20–0.35 for Chesapeake Bay.

		Yield-per-recruit (g)					Yield-per-recruit (g)		
M	t_c	F = 0.75	F_{MAX}	% increase	M	t_c	F = 0.75	F_{MAX}	% increase
0.20	1	160.4	168.9	5.3	0.30	1	129.2	142.5	10.3
	2	153.9	165.1	7.3		2	112.8	128.9	14.3
	3	140.3	154.1	9.8		3	93.4	109.0	16.7
	4	123.5	137.8	11.6		4	74.6	88.2	18.2
	5	106.3	119.8	12.7		5	58.2	69.4	19.2
0.25	1	143.7	153.5	6.8	0.35	1	116.5	132.4	13.6
	2	131.6	145.8	10.8		2	97.0	114.0	17.5
	3	114.3	129.5	13.3		3	76.5	91.7	19.9
	4	95.8	110.3	15.1		4	58.1	70.7	21.7
	5	78.5	91.2	16.2		5	43.1	52.9	22.7

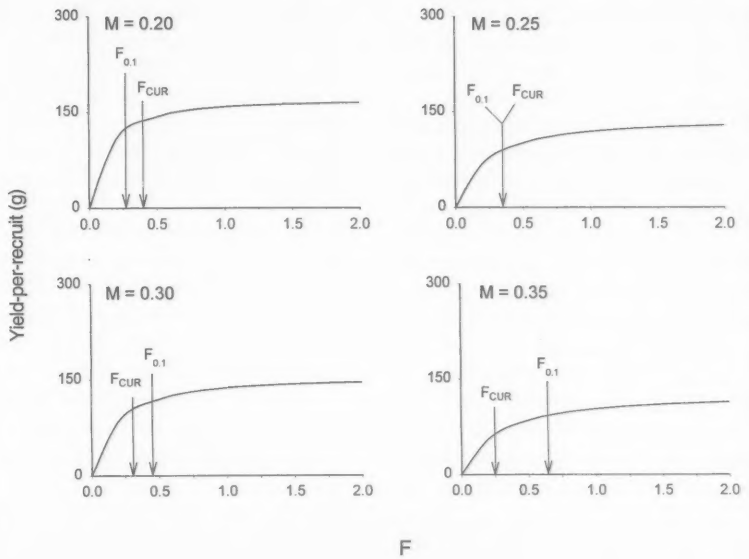

Figure 2

Curves of yield-per-recruit on fishing mortality (F) for Atlantic croaker, *Micropogonias undulatus*, in the lower Chesapeake Bay (period 1988–91) estimated for mean age-at-first-capture (t_c) = 2 and natural mortality (M) = 0.20–0.35. $F_{0.1}$ = the level of F at which the marginal increase in yield-per-recruit due to a small increase in F is 10% of the marginal yield-per-recruit in a lightly exploited fishery; F_{CUR} = the estimated current levels of fishing mortality.

the level of $F_{0.1}$ (Fig. 2; Table 3). For M = 0.20, F_{CUR} is higher than $F_{0.1}$, indicating that, although it produces slightly higher yield values, current fishing mortality is not at its most economically efficient level. For example, for t_c = 1 and t_c = 2, over 90% of the yield obtained at F_{CUR} can be achieved by lowering fishing mortality to the level of $F_{0.1}$. For M = 0.25, both F_{CUR} and $F_{0.1}$ equal 0.35, indicating that, although below the maximum potential yield-per-recruit, estimated current levels of harvest probably correspond to the most efficient level of F. In contrast, if M ranges from 0.30 to 0.35, $F_{0.1}$ is higher than F_{CUR} (Table 3), suggesting there would still be room to increase yield efficiently with increases in F. However, at these higher levels of M, increases in F necessary to achieve the yields at $F_{0.1}$ may be unrealistically high (Table 3).

Values of t_{CRITIC} estimated with different values of M were relatively low for Atlantic croaker in Chesapeake Bay. For M equal to 0.20, 0.25, 0.30, and 0.35, values of t_{CRITIC} were 1.9, 1.4, 1.0, and 0.6 years, respectively. These values indicate that, for the range of M considered herein, maximum theoretical cohort biomass in the absence of fishing would be achieved before Atlantic croaker reach age 2 (years).

Table 3

Estimated value of current levels of fishing mortality (F_{CUR}) and level of fishing mortality at which the marginal increase in yield-per-recruit due to a small increase in F is 10% of the marginal yield-per-recruit in a lightly exploited fishery ($F_{0.1}$) for Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay region for a range of fishing mortality (M) = 0.20–0.35, and the percent increase or decrease in F_{CUR} necessary to make it equal to $F_{0.1}$.

M	F_{CUR}	$F_{0.1}$	% Difference
0.20	0.40	0.27	–48
0.25	0.35	0.35	0
0.30	0.30	0.45	+50
0.35	0.25	0.64	+156

Estimated values of P_g for Atlantic croaker in Chesapeake Bay were also relatively low. For L_∞ = 312 mm, and the current estimated level of l_c (265 mm, corresponding to t_c=2), P_g = 0.15, i.e., on the average, only 15% of their potential growth still remains when Atlantic croaker in Chesapeake Bay enter the exploited phase at age 2. For alternative values of t_c

equal to 1, 3, 4 and 5 years, values of P_g are 0.21, 0.10, 0.07, and 0.05, respectively.

North Carolina

Curves of yield-per-recruit on F for Atlantic croaker in North Carolina (Fig. 3) showed an opposite trend from that shown in Chesapeake Bay. For all levels of F or M used in simulations, yield values continuously increased from t_c = 1 (177 mm TL) to t_c = 5 (434 mm TL), indicating that yield could be maximized by increasing t_c. However, the shape of yield-per-recruit curves differed among different levels of M and t_c (Fig. 3). For M = 0.20 and 0.25, curves for t_c = 1–3 peaked at low to intermediate levels of F (F_{MAX} = 0.20–0.60) and gradually decreased after that, whereas for t_c = 4–5 they increased rapidly in the range of F between 0 and 0.35–0.60 and remained relatively flat thereafter. For M = 0.30–0.35, the peaks in yield at low to intermediate levels of F occurred only for t_c = 1–2 and were a lot less pronounced than those at lower levels of M.

For the range of M used in our simulations, estimates of F_{CUR} (Fig. 4) indicated that during the period 1979–81 the level of fishing mortality for Atlantic croaker in North Carolina was well above the levels of $F_{0.1}$ and F_{MAX}. At t_c = 1, estimated losses in potential yield-per-recruit from F_{MAX} to F_{CUR} were equal to 45%, 35%, 25%, and 4% for M = 0.20, 0.25, 0.30, and 0.35, respectively. Estimated losses if fishing mortality were kept at the level of $F_{0.1}$ would be 44%, 22%, 20%, and 14%, respectively.

Estimated values of t_{CRITIC} and P_g for Atlantic croaker in North Carolina were much higher than those estimated for Chesapeake Bay. For M equal to 0.20, 0.25, 0.30, and 0.35, values of t_{CRITIC} were 7.5,

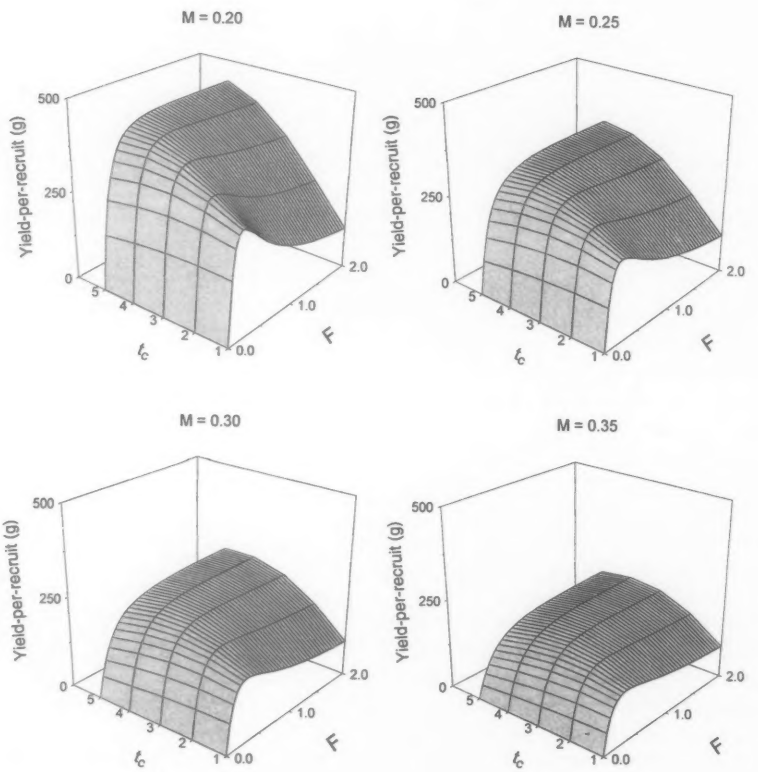

Figure 3

Curves of yield-per-recruit on fishing mortality (F) for Atlantic croaker, *Micropogonias undulatus*, in North Carolina (period 1979–81) estimated for mean age-at-first-capture (t_c) = 1–5 and natural mortality (M) = 0.20–0.35.

6.7, 6.1, and 5.6 years, respectively. For L_∞ = 645 mm and the estimated level of l_c for the period 1979–81 (177 mm, corresponding to t_c=1), P_g = 0.72, i.e., on the average, 72% of their potential growth still remained when Atlantic croaker in North Carolina entered the exploited phase at age 1 during the period 1979–81. For alternative values of t_c = 2–5 years, values of P_g were 0.59, 0.49, 0.39, and 0.33, respectively.

Discussion

Our modeling results indicate that, for the range of M and F used in simulations, yield-per-recruit of Atlantic croaker in the lower Chesapeake Bay could be maximized by a management strategy that incorporates early age at first capture (t_c=1) and high rates of fishing mortality (F=2.0). However, the analysis for Chesapeake Bay also showed this is probably not the most efficient management option for this species. Because of the essentially asymptotic relation between yield-per-recruit and F, harvesting Atlantic croaker at or near their maximum potential yield (i.e. at F_{MAX}) would require a disproportionate increase in fishing mortality making it an economically inefficient management option. In addition, given the multispecies nature of the main fisheries for Atlantic croaker in Chesapeake Bay (Austin, 1987; Chittenden, 1991), raising current levels of F would greatly increase overall rates of exploitation and probably interfere with management of other species such as weakfish, *Cynoscion regalis*, and spot, *Leiostomus xanthurus*.

Decreasing the current level of t_c for Atlantic croaker in Chesapeake Bay would not be recommended for two reasons. First, for the range of M used in simulations, gains in yield-per-recruit from t_c = 2 to t_c = 1 were relatively small at F_{CUR}. Second, because of the magnitude of the scrap catch of Atlantic croaker in Chesapeake Bay (Mercer[1]), it is likely that this species is already entering the exploited phase at age 1 or younger. The current estimate of t_c (t_c=2; Barbieri et al., 1994a) may be an overestimate because it was based on arbitrarily defined commercial market grades instead of overall catches—including the scrap. Because the market accepts only fish above a certain size, a reduction in mesh sizes to attempt to increase the proportion of age-1 Atlantic croaker in the catches would probably only increase the number of fish sold as scrap and have little or no effect on commercial market grades.

Nevertheless, the analysis showed no indication that fully recruited Atlantic croaker in Chesapeake Bay are being growth-overfished (i.e. that the fish were being caught before they had a chance to grow to their ideal size). Yield-per-recruit modeling results and estimated values of F_{CUR} indicated that, over a likely range of M, current levels of harvest are below the levels at F_{MAX} and, under most scenarios, at or below the levels at $F_{0.1}$. In addition, yield-per-recruit curves showed no signs of decrease at higher levels of F, even if M is as low as 0.20. This pattern suggests that stocks of Atlantic croaker in the Chesapeake Bay region show the same great biologi-

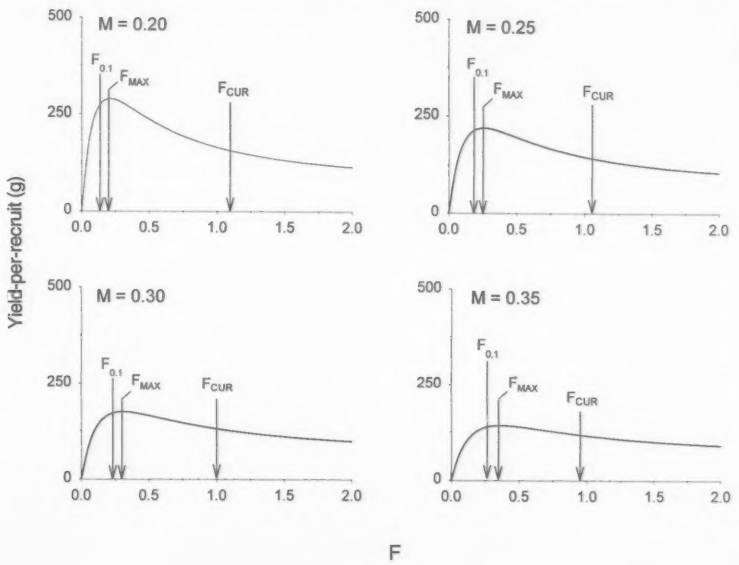

Figure 4

Curves of yield-per-recruit on fishing mortality (F) for Atlantic croaker, *Micropogonias undulatus*, in North Carolina (period 1979–81) estimated for mean age-at-first-capture (t_c) = 1 and natural mortality (M) = 0.20–0.35. $F_{0.1}$ = the level of F at which the marginal increase in yield-per-recruit due to a small increase in F is 10% of the marginal yield-per-recruit in a lightly exploited fishery; F_{CUR} = the estimated current levels of fishing mortality.

cal capacity to resist growth overfishing as those stocks in the northwestern Gulf of Mexico (Chittenden, 1977). The low values of t_{CRITIC} and P_g agree with yield-per-recruit modeling results and indicate that 1) for a reported maximum longevity of 8 years in Chesapeake Bay (Barbieri et al., 1994a), maximum theoretical biomass is achieved very early in life, before fish reach age 2; and 2) very little potential for a growth span still remains when fish enter the exploited phase at age 2. As a precaution against future problems—especially considering that annual recruitment is reported to be highly variable and strongly density independent—we suggest that regulatory measures for Atlantic croaker in the lower Chesapeake Bay be directed at maintaining the apparent current level of t_c (age 2; l_c=265 mm TL; Barbieri et al., 1994a). In addition, the magnitude and composition of the scrap catch for the main fisheries in this area need to be estimated, and their effect on estimates of F_{CUR} and t_c need to be assessed more precisely before any definite conclusion on Atlantic croaker yield-per-recruit can be reached.

In contrast to what we found for the lower Chesapeake Bay, results for North Carolina indicated that Atlantic croaker were being severely growth-overfished. First, independent of the level of F or M used in simulations, yield-per-recruit values were consistently higher at higher levels of t_c, indicating that age and size limits during the period 1979–81 (t_c=1, l_c=177 mm TL; Ross, 1988) were unrealistically low. Second, estimates of F_{CUR} for t_c = 1 were not just consistently higher than $F_{0.1}$ but were also well above F_{MAX}. The pattern of declining yield-per-recruit values with increasing F at lower levels of t_c agrees well with the high estimates of t_{CRITIC} and P_g and indicates that, contrary to the pattern shown in Chesapeake Bay, maximum cohort biomass is attained later in life (ages 5–7).

However, differences in yield-per-recruit modeling results between Chesapeake Bay and North Carolina seem to reflect temporal rather than spatial differences in Atlantic croaker population dynamics. Parameters used in simulations for North Carolina were obtained from a study (Ross, 1988) conducted during a period (1979–81) that coincides with the occurrence of unusually large Atlantic croaker (350–520 mm TL; Ross, 1988) along the east coast of the United States (Barbieri et al., 1994a). However, since 1982, Atlantic croaker catches in North Carolina have been dominated by smaller fish. Modal lengths of Atlantic croaker in the long haul-seine fishery during 1982-92 ranged from 215 to 245 mm TL; in the winter trawl fishery, they ranged from 215 to 240 mm TL. In both fisheries, less than 10% of the fish were older than age 3 (Wilson, 1993). Therefore, yield-per-recruit modeling results presented here for North Carolina should not reflect current conditions, but rather be considered representative of temporal changes in Atlantic croaker population dynamics.

The specific value of M used in our simulations had no effect on the levels of F or t_c that produce maximum yield-per-recruit values and would not change conclusions for either Chesapeake Bay or North Carolina. However, these conclusions are still critically dependent on how realistic is the range of M used in these simulations. Methods currently used to estimate M have strong limitations and disadvantages (Vetter, 1988), and the method used here is no exception. However, we feel comfortable with the range of M used in this study because it agrees with values of M reported for other sciaenids with similar life spans, e.g. spotted seatrout, *Cynoscion nebulosus* (Rutherford et al., 1989).

Yield-per-recruit analysis is only part of a fishery management strategy (Beverton and Holt, 1957; Gulland, 1983; Deriso, 1987). It must be applied in conjunction with eggs-per-recruit (Prager et al., 1987) and spawning stock biomass per recruit models (Gabriel et al., 1989; Goodyear, 1993; Schirripa and Goodyear, 1994) to allow managers to examine the effects of different policies on both reproduction (i.e. egg production) and biomass yield. The pattern of early maturation, multiple spawning, long spawning season, and indeterminate fecundity in Atlantic croaker (Barbieri et al., 1994b) suggest that reproduction would be compromised only at extremely high levels of fishing. However, eggs-per-recruit and spawning stock biomass models must be applied before this issue can be properly evaluated.

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Abstract.—Eight female cunners, *Tautogolabrus adspersus*, were tagged externally with ultrasonic transmitters in Newfoundland, and their activity pattern was recorded. They were active diurnally, commencing activity, on average, 55 minutes after sunrise and ceasing activity about 50 minutes after sunset. The diurnal activity period was interrupted by periods of inactivity usually lasting 5–15 minutes. Levels of activity varied daily and seasonally; seasonal changes were the most dramatic. On average, female cunners were active for more than 12.5 h/day in June–July and for only 3 h/day in October–November. Decrease in activity reflected decreasing day length; as photoperiod became shorter, cunners spent a much larger portion of the daylight period inactive (22.9% in June–July compared with 71.8% in October–November). Decrease in cunner activity in the fall occurred while water temperature was as high as that in June and July and is speculated to be controlled by an endogenous rhythm.

Daily and seasonal activity patterns of female cunner, *Tautogolabrus adspersus* (Labridae), in Newfoundland

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Cunner, *Tautogolabrus adspersus*, is the most northerly distributed labrid fish in the western North Atlantic, reaching the northern extent of its range in waters off Newfoundland. A member of a large, essentially tropical, family, it is well known for its annual state of prolonged physiological torpor, which in Newfoundland may last for more than 6 months (Green and Farwell, 1971). The ability of cunners to undergo a long period of torpor is apparently one of the factors that have enabled this species to flourish in a low temperature environment (Curran, 1992). In waters off Newfoundland, cunners are abundant and inhabit sites where summer maximum water temperature is less than 11°C and the winter minimum is below –1°C. Newfoundland cunners enter and remain in torpor when seawater temperature is below about 5°C (Green and Farwell, 1971).

Throughout their range, Chesapeake Bay to the Strait of Belle Isle, cunners are associated with inshore habitats that provide shelter during nocturnal quiescence (a characteristic of labrids) as well as during overwintering torpor (Pottle and Green, 1979a). Rather than migrating to deeper, warmer water as the temperature declines in the fall, Newfoundland cunners take shelter under boulders and rocks at their summer feeding and reproductive sites. There they remain until the seawater temperature approaches 5°C the following year, usually in early June (Green and Farwell, 1971). In Conception Bay, Newfoundland, territorial males establish territories within a week of emerging from winter torpor and maintain them until just prior to reentering winter torpor, usually in late November or early December (Pottle and Green, 1979a). Spawning commences in mid to late July, depending upon water temperature, and lasts for 2–3 weeks. All spawning activity occurs within male territories (Pottle and Green, 1979b; Martel and Green, 1987).

We recently reported on a home-range size for adult female cunners in Conception Bay, Newfoundland, that was based on telemetry data

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from fish tagged with ultrasonic transmitters (Bradbury et al., 1995). Female cunners occupy small home ranges (300–2,353 m^2) and exhibit seasonal variation in the size of their home range. The largest home ranges occur during June and July, a time when cunners are replacing energy stores depleted during winter torpor (Bradbury et al., 1995). This is also the time of year with the longest photoperiod and hence with the maximum potential foraging period for a diurnal species.

In this study, we report on the daily activity patterns of the female cunners in Conception Bay. Cunners at the northern extent of their range are of interest because their prolonged winter torpor may reduce annual foraging time. We expected that as the photoperiod decreased, female cunners would be active for more of the diurnal period, both to maximize growth and increase energy stores in preparation for six months of winter torpor.

Table 1

Total length and tracking dates for female cunner tagged with ultrasonic transmitters in Broad Cove, Conception Bay, Newfoundland.

Fish identification	Total length (mm)	Tracking dates	Track duration (days)
A	194	17 Jun–30 Jun	14
		5 Jul–6 Jul	2
B	215	18 Jun–4 Jul	17
C	250	28 Jun–21 Jul	24
D	235	12 Jul–21 Jul	10
E	195	15 Aug–18 Aug	4
F	225	30 Aug–22 Sep	16
G	245	23 Sep–20 Oct	22
H	240	21 Oct –24 Nov	32

Methods

Tracking

A fixed hydrophone array tracking system (Bradbury et al., 1995) was used to monitor the activity of eight female cunners tagged with ultrasonic transmitters in Broad Cove, Conception Bay. The system provided positional information (fixes) on a tagged fish once every 15 seconds. The change in the quality of the transmitter signal when a tagged cunner sought shelter by going under a boulder or into a crevice between two rocks enabled us to monitor activity-inactivity patterns accurately in much the same way as Chapman et al. (1975) had done with Norway lobster (*Nephrops norvegicus*). For a description of the tracking system, tagging procedure, and study site see Bradbury et al. (1995). With our tagging procedure, a tag holder and dummy tag were initially attached to fish in the field. After a week (minimum period), a fish with a tag holder and dummy tag was recaught by a diver, and the dummy transmitter was replaced with a functional one. The latter procedure involved handling the fish for 1–2 min, from capture to release.

Tagged cunners were from 194 to 250 mm in total length (Table 1). At this size female cunners in Conception Bay are sexually mature (Pottle and Green, 1979a). Fish were tracked from June until November, i.e. during most of the period between the end and start of winter torpor. Lightning damage to the tracking system limited the amount of tracking that could be done in August. Individual fish were tracked for 4 to 32 days during which they all remained in the area encompassed by the hydrophone array. For the duration of the tracking period, information on water temperature, sea state, tidal phase, and cloud cover was available on a daily basis, as described by Bradbury et al. (1995).

Activity-inactivity

A tagged cunner was determined to be active or inactive based on information from the tracking system. If a strong transmitter signal was received, and positional information was obtained, the subject was considered active. If, on the other hand, signals were weak and no positional fix could be determined for more than 3 min (12 possible fixes), the fish was considered inactive. With scuba or snorkel equipment, divers documented over a period of >20 h that cunners had retreated into cracks and crevices or underneath objects when transmitter reception was poor. These observations also showed that female cunners do not "rest" on the substrate in open sites.

During the night, cunners seek shelter and undergo a period of nocturnal quiescence during which positional fixes cannot be obtained. The first and last positional fixes of the day therefore marked the beginning and end of diurnal activity. Onset of diurnal activity was expressed as the number of minutes before or after sunrise, whereas cessation of diurnal activity was expressed as the number of minutes before or after sunset. The duration of diurnal activity for an individual was defined as the total elapsed time between the onset and cessation of its daily activity.

Cunners also entered shelter (became inactive) at various times throughout the day; sites where cunners were inactive are termed day-rest sites. The duration of each inactive period (the time between

the initiation and the end of a poor transmitter signal) was recorded. On the basis of these data, the portion of the diurnal activity period spent inactive was calculated and expressed as a percentage.

In describing the activity-inactivity patterns of female cunners, five parameters were used: 1) onset of activity, 2) cessation of activity, 3) duration of diurnal activity, 4) length of inactivity bouts, and 5) percent of diurnal activity period spent inactive.

Analysis of data

Although a fish was handled for only 1–2 min when a transmitter was inserted into its tag holder and although field observations did not detect any changes in the behavior of fish following this procedure, nonparametric paired *t*-tests were used to examine whether female cunners showed similar activity on the first complete day of tracking (day 2) compared with the following day of tracking (day 3). All five activity parameters were tested.

A nonparametric analysis (Wilcoxon matched-pairs signed-ranks test) was used to compare interindividual differences in activity between the two pairs of subjects tracked during the same periods (Table 1). Comparisons were made between fish A and fish B for a total of 11 days (i.e. June 18, 19, 20, 21, 22, 24, 25, 27, 28, 29, and 30) and between fish C and fish D for a total of 9 days (i.e. July 13–21 inclusive) for all five activity parameters.

A least-squares multiple regression analysis was used to determine whether date, time of day (i.e. morning vs. afternoon), or environmental variables (water temperature, cloud cover, and sea state) had a significant effect on activity. All activity parameters were tested. Because the activity data were normally distributed, no transformations were carried out. Although there were 141 tracking days, some days could not be used for certain activity parameters. For example, there were only 72 tracking days during which both the time of onset and cessation of activity were known for any given fish, both of which are required to calculate the duration of diurnal activity.

The tidal cycle was divided into four phases: low-tide, flood-tide, high-tide, and ebb-tide as described by Bradbury et al. (1995). For fish A, B, C, and D, mean activity parameters (i.e. percentage of time spent inactive and length of inactivity bouts) were determined for each tidal phase for the duration of the tracking period. An analysis of variance with three factors was used to test for intra- and interindividual differences in activity during the tidal phases. We included only the fish by tide interaction term in our analyses because we did not expect any temporal variation in tide (tide × date) or activity (fish × date), given the relatively short time (i.e. 11 and 9 days) over which observations were made.

Table 2

Mean number of minutes before sunrise and after sunset when tracked female cunners began and ceased their diurnal activity. Because the data for onset of activity for fish E consisted of a single point, no standard deviation is given.

Fish identification	Onset (minutes before sunrise)			Cessation (minutes after sunset)		
	Mean	SD	*n*	Mean	SD	*n*
A	57.6	10.02	9	57.6	26.70	9
B	40.2	23.95	12	63.6	18.10	12
C	48.7	10.93	18	74.3	19.64	22
D	31.7	18.48	6	43.0	43.59	4
E	45.0	—	1	50.3	34.46	4
F	52.0	21.28	3	36.5	41.16	4
G	49.4	32.69	14	54.1	20.33	17
H	72.4	52.54	28	18.9	39.12	27
All	54.7	36.63	91	49.1	36.15	99

Paired comparison *t*-tests were used to examine whether the one female cunner tracked during both the prespawning and spawning period had the same activity patterns during both periods. All activity parameters were tested.

Statistical analyses were performed with Minitab (Minitab, Inc., 1992) or SPSSX (SPSS Inc., 1990) statistical software packages.

Results

There were no significant differences ($P>0.05$, nonparametric paired *t*-test) in activity parameters between the first complete day of tracking (day 2) and the following day.

All tagged fish were active during the day, inactive at night. Activity commenced, on average, 55 minutes (SD=36.6) before sunrise and ceased 49 minutes (SD=36.2) after sunset; however, there was considerable daily variation among individuals (Table 2). Throughout the day, activity was interrupted by periods of inactivity, usually lasting 5–15 minutes. Among those fish tracked on the same day, there were no significant differences between subjects for any of the activity parameters (Table 3).

When water temperature was below 5°C, cunners were inactive. On 23 and 24 June, for example, strong northwesterly winds forced cold water into the study area causing the water temperature to drop from 6°C to 3°C and the cunners to be inactive for two days. On the morning of 26 June the water temperature

Table 3

Results of the Wilcoxon matched-pairs signed-ranks test (t-value) used to compare interindividual differences in activity between pairs of cunners tracked during the same periods (n represents the number of days during which comparisons were made). Critical values of t are derived from Rohlf and Sokal (1969). There were no significant differences between fish for any of the activity parameters tested.

	Comparisons between fish A and fish B			Comparison between fish C and fish D		
Behavioral parameter	n	t-value	Critical t-value (significance level)	n	t-value	Critical t-value (significance level)
Percent of time inactive	11	26	13 (0.0415) 14 (0.0508)	9	11	8 (0.0488) 9 (0.0645)
Length of inactivity bout	11	26	13 (0.0415) 14 (0.0508)	9	14	8 (0.0488) 9 (0.0645)
Onset of activity	9	15	8 (0.0488) 9 (0.0645)	7	6	3 (0.0391) 4 (0.0547)
Cessation of activity	8	10	5 (0.0391) 6 (0.0547)	7	5	3 (0.0391) 4 (0.0547)
Duration of diurnal activity	8	13	5 (0.0391) 6 (0.0547)	7	7	3 (0.0391) 4 (0.0547)

Table 4

Summary of multiple regression analysis on the effects of time of day (prior to 1200 h vs. after 1200 h), date, and environmental variables on activity of female cunner. A minimum of 62 days and a maximum of 89 days were incorporated in the regression analysis for the last three behavioral parameters. Percentage of variation accounted for by each variable is given. * = significant at 0.05 level; ** = significant at 0.01 level; and *** = significant at 0.001 level.

Behavioral parameter	n	Time of day	Date	Water temperature >5°C	Sea state	Cloud cover	Combined variables
Percent of time inactive	205	0.6	58.7***	0.2	0.3	0.1	59.9***
Length of inactivity bout	229	0.1	12.7***	2.8**	1.7*	0.2	17.5***
Onset of activity	75	NA	6.6*	1.9	0.0	0.1	8.6
Cessation of activity	83	NA	22.3***	0.2	0.0	0.5	23.0***
Duration of diurnal activity	62	NA	92.3***	0.9**	0.1	0.1	93.4***

again dropped to 3°C, resulting in cunners being inactive for the remainder of the day. Temperatures above 5°C had small but significant effects on length of inactivity bouts and duration of diurnal activity (Table 4). Length of bouts of inactivity tended to decrease with increasing water temperature, whereas the trend was reversed for the duration of diurnal activity. Water temperatures above 5°C had no significant effect on the onset or cessation of activity or on the percentage of time spent inactive.

Sea state had a significant ($P<0.05$) effect on length of cunner inactivity bouts (Table 4), with bouts of inactivity tending to be longer on days with high surface waves. Sea state did not have a significant effect on other activity parameters. Cloud cover had no significant effect on any of the activity parameters. There was a trend, however, for females to remain inactive for longer periods (i.e. percentage of time spent inactive increased as well as length of inactivity bouts) as cloud cover increased. There was also a tendency for the duration of diurnal activity to decrease with increasing cloud cover. Neither percentage of diurnal activity period spent inactive or length of inactivity bouts differed between morning and afternoon (Table 4).

There was no significant difference in fish behavior owing to tides (Table 5), indicating that both fish A and fish B responded similarly to the tidal cycle. Furthermore, there was no significant difference in activity (i.e. percentage of time spent inactive) between the various tidal phases for fish A or fish B (Table 5). Finally, there were no significant differ-

Table 5

Results of analysis of variance performed on the percentage of time spent inactive by fish A and fish B during the four phases of the tidal cycle. df = degrees of freedom; SS = sum of squares; MS = mean of squares.

Source	df	SS	MS	*F*-value	Probability value *P*
Date	10	5,492.5	549.3	1.74	0.089
Fish	1	33.1	33.1	0.10	0.747
Tide	3	1,320.8	440.3	1.39	0.252
Fish × tide	3	771.5	257.2	0.81	0.490
Error	70	22,117.3	316.0		
Total	87	29,735.3			

ences between the tidal phases for the length of inactivity bouts of fish A and fish B ($F_{3,70}$=1.57, P=0.204; $F_{1,3}$=0.4, P=0.756), percent of time spent inactive by fish C and fish D ($F_{3,56}$=0.50, P=0.685; $F_{1,3}$=0.79, P=0.505) and length of inactivity bouts of fish C and fish D ($F_{3,56}$=0.82, P=0.4986; $F_{1,3}$=1.94, P=0.134).

Time of year, i.e. seasonal factors, accounted for 58.7% of the variation in the percentage of the diurnal activity period spent inactive, i.e. the amount of time spent in shelter between the commencement and cessation of daily activity (Table 4). Cunners spent an increasing proportion of the diurnal period inactive from June through November. This factor accounted for 12.7% of the variation in length of inactivity bouts (which increased over time as well) and for 6.6% and 22.3% of the variance in onset and cessation of activity, respectively (Table 4). The trend was for activity to begin later in the morning and to end earlier in the evening (in relation to sunrise and sunset) as the season progressed. Time of year accounted for 92.3% of the variation in duration of diurnal activity. As the seasons progressed and the photoperiod became progressively shorter, there was a corresponding decrease in the duration of diurnal activity (Fig. 1).

Thus the duration of cunner diurnal activity, percentage of time inactive, and length of inactivity bouts were all closely related to day length. By combining data from all subjects, the average elapsed time between onset and cessation of activity (i.e. duration of diurnal activity) was 16.5 h (n=38, SE=0.10) during June–July, 13.5 h (n=8, SE=0.19) during August–September, and 11.0 h (n=27, SE=0.25) during October–November. Cunner spent 22.9% (n=35, SE=15.5) of the diurnal period inactive between June and July, 47.0% (n=13, SE 24.3) of the diurnal period inactive in August–September, and 71.8% (n=30, SE=13.2) of the diurnal period inactive during October–November; length of inactivity bouts, on the other hand, increased from an average of 6.4 min (n=64, SE=0.75) in June–July to 9.3 min (n=15, SE 1.56) in August–September, to 12.7 min (n=41, SE=1.14) in October–November.

These data were used to calculate the number of hours a female cunner spent out of its shelter per day. On average, during June–July, female cunners were active for 12.5 h/day, during August–September 7 h/day, and during October–November only 3 h/day. The remainder of the year was spent in winter torpor.

There were no significant differences (P>0.05, paired comparison t-test) in any of the activity parameters for the single female cunner tracked during both the prespawning and spawning periods.

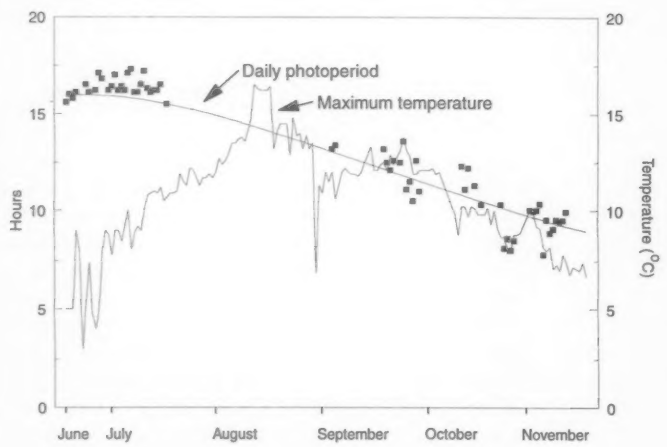

Figure 1

Relation between length of daily photoperiod and duration of diurnal activity (■) for eight female cunners tracked in Conception Bay, Newfoundland, between June 17 and November 24. Maximum daily seawater temperature at the study site is also shown.

Discussion

Pottle (1979) reported that in Newfoundland territorial male cunners undergo periods of daylight quiescence under cover. Whoriskey (1983) also observed cunners in Massachusetts underneath boulders at those times during the day when they were

not foraging. The female cunners we studied exhibited similar behavior, seeking shelter beneath rocks or in crevices during the day.

Some workers have assumed that temperate wrasses use cover to avoid predation (Olla et al., 1979; Hobson et al., 1981), although threat of predation has not been well documented as a factor. Whoriskey (1983) interpreted the diurnal use of shelter by cunners in Massachusetts as predator avoidance. Although he may have been correct, our field observations in Newfoundland do not support this hypothesis. Predation on adult cunners in Conception Bay is very low as judged by over 400 hours of diving observations during which no predation, or attempted predation, on adults was observed.

Females may seek shelter to avoid conspecifics with courting and chasing behaviors, especially territorial males. This explanation, however, is inadequate in elucidating why males exhibit the same behavior or why the behavior occurs so frequently outside the spawning period.

A reduction in energy expenditure may be associated with such behavior because cunners probably require less energy to maintain a position in a shelter than in the water column, even when water movement from currents and waves is minimal, and because the length of inactivity bouts increased with increased water turbulence. However, such an explanation is weak unless it can be shown that continued foraging would result in a net loss of energy.

In many diurnal fishes, including cunners, the onset and cessation of daily activity coincides closely with the rising and setting of the sun (e.g. Hobson, 1972, 1973; Hawkins et al., 1974; Olla et al., 1974, 1975; Clark and Green, 1990). As expected, females exhibited a marked seasonal decrease in the duration of their diurnal activity (from 16.5 h in June–July to 11.0 h in October–November) as day length decreased. Light intensity at sunrise and sunset was affected seasonally by the surrounding topography at the study site (e.g. in the fall the sun "set" behind a range of hills rather than at sea level), and this topography may have accounted for some of the seasonal change in the onset and cessation of diurnal activity. However, the considerable variation in the onset and cessation of daily activity among cunners suggests that this variation is not simply a response to a threshold light intensity.

Contrary to the expectation that female cunners would maximize foraging opportunities prior to entering winter torpor, they spent a larger percentage of the diurnal period inactive as the length of the photoperiod decreased. Why cunners should significantly reduce their foraging activity, at a time when food is still available and they could acquire more energy for somatic growth and winter torpor, is not clear. Although water temperature is decreasing during this period, our analyses show that above ~5°C, temperature has little direct effect in determining the ratio of activity to inactivity. Mean daily water temperatures during June–July and October–November were approximately the same (8.2°C and 9.2°C, respectively)(Fig. 1), yet there were large differences in the amount of time cunners spent in shelter. During June and July, females were outside their shelter for about 12.5 hours of the day, whereas from October to November cunners were active, on average, only 3 hours of the 11-h sunrise to sunset period.

Fall or winter decreases in the activity or feeding behavior (or both) of fishes in the absence of changes in water temperature are common, although the mechanisms underlying these decreases are not understood. Smith et al. (1993) for example found that in Atlantic salmon (*Salmo salar*), seasonal reductions in swimming activity and feeding were more closely related to day length and changes in day length than to other environmental variables, including water temperature. This also seems to be true for cunners. Presumably their temporal pattern of activity is adaptive and important to their success at northern latitudes. Cunners survive six months or more of torpor that can begin at a time not predictable by exogenous cues in the marine environment. At our study site, the date at which winter torpor commences (i.e. when seawater temperature remains below ~5°C) can vary year to year by at least four weeks. Perhaps an endogenous mechanism sensitive to changes in day length, or to some other environmental cue, regulates the physiological processes associated with successful winter torpor. Although such a mechanism may exist in cunners, the identification of endogenous rhythms in fishes is difficult (Boujard and Leatherland, 1992).

Our findings concerning seasonal changes in the activity patterns of cunners have implications for estimating the size of their populations. For example, population estimates based on visual surveys by divers should take into account that, depending on when the survey is conducted, a significant and variable proportion of the population will be out of sight, under cover. Significant errors in estimates of population size are likely, and errors will not be consistent for different times of the year. This caution may apply to other species with similar behavior patterns.

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The composite square-mesh panel: a modification to codends for reducing unwanted bycatch and increasing catches of prawns throughout the New South Wales oceanic prawn-trawl fishery

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Abstract.—The effectiveness of a new bycatch reduction device (BRD) was tested across a wide geographical range to determine its use in the NSW oceanic prawn-trawl fishery. Using four commercial trawlers, each from a different port located in the fishery, we compared the catches and bycatches from conventional trawls with those from trawls containing composite panels of netting (60 mm and 40 mm) hung on the bar and inserted into the top anterior section of the codend (termed the composite-panel codend). This panel was designed so that the 40-mm mesh 1) would allow some small fish to escape and 2) would distribute the load anterior and lateral to the 60-mm mesh (which was located in an area where waterflow was thought to be greatest), allowing the 60-mm mesh to remain open and thus facilitate the removal of larger fish. Simultaneous comparisons against a control codend showed that the composite-panel codend significantly reduced the weights of discarded bycatch at all four locations (means reduced by 23.5% to 41%) and the numbers of juveniles of commercially important species, such as whiting, *Sillago* sp. (by up to 70%). At three of the locations the composite-panel significantly increased the catches of the prawn *Penaeus plebejus* (5.5% to 14%) and, although not statistically significant, showed a similar trend at the fourth location (mean increase of 4%). As a result of this study, the composite-panel codend has been adopted and voluntarily used by fishermen throughout the New South Wales oceanic prawn-trawl fishery.

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In New South Wales (NSW), Australia, oceanic prawn-trawling involves over 300 vessels operating from 11 major ports along 1,000 km of coastline and is valued at approximately A$17 million per annum. Vessels operating in this fishery primarily target the eastern king prawn, *Penaeus plebejus*, although a significant portion of the total value in the fishery is derived from the sale of legally retained bycatch (termed "by-product")—comprising several species of fish, crustaceans, and cephalopods. As in the majority of the world's prawn-trawl fisheries, however, significant numbers of nontarget organisms are also captured and discarded in this fishery (for reviews see Saila, 1983; Andrew and Pepperell, 1992; Alverson et al., 1994; Kennelly, 1995). In NSW, this discarded bycatch includes individuals of byproduct species that are smaller than the minimum commercial size and a large assemblage of noncommercial species (see Kennelly, 1995).

Unwanted bycatch has been reduced in several of the world's prawn-trawl fisheries by means of modifications to codends that contain bycatch reduction devices (BRD's) (e.g. Watson et al., 1986; Matsuoka and Kan, 1991; Isaksen et al., 1992; Rulifson et al., 1992; Renaud et al., 1993; Christian and Harrington[1]). In general, these modifications have involved either 1) some form of rigid structure that functions by mechanically separating larger unwanted individuals or 2) a strategically placed escape "window" made of netting that works by exploiting behavioral differences between prawns and smaller finfish. Although many of these modifications have proven effective in reducing bycatch from prawn trawls, sometimes they have not been favored by commercial fishermen (see Kendall, 1990; Renaud et al., 1993) because of their size (in relation to the codend), their often complex design (e.g. Mounsey et al., 1995), and, in some cases, their failure to maintain prawn catches at the same levels as conventional trawls (e.g. Rulifson et al., 1992; Robins-Troeger et al., 1995; Christian and Harrington[1]).

One modification that has been successfully tested and adopted in

[1] Christian, P., and D. Harrington. 1987. Loggerhead turtle, finfish and shrimp retention studies on four excluder devices (TEDs). *In* Proceedings of the nongame and endangered wildlife symposium; 8–10 September 1987, Georgia, p. 114–127. Dep. Nat. Resources, Social Circle, GA.

several trawl fisheries in the North Atlantic involves inserting large panels of square-mesh in codends (Robertson and Stewart, 1988; Carr, 1989; Briggs, 1992; Isaksen and Valdermarsen[2]; Suuronen[3]). These studies have shown that square-mesh panels often reduce the bycatch of juvenile roundfish while retaining a large proportion of the targeted catch. In previous experiments (Broadhurst and Kennelly, 1994, 1995, 1996; Broadhurst et al., 1996), we have shown that relatively small panels of square-mesh, inserted into the top anterior sections of penaeid prawn-trawl codends, allowed large numbers of small fish to escape without any losses of prawns. In these experiments, the majority of fish were thought to have been herded together in the narrow anterior section of the codend, immediately in front of the catch (see also Wardle, 1983). This concentration of fish was thought to upset the balance of the school and to initiate a response in the fish to escape by swimming towards the sides and top of the net and out through the open square-meshes. In addition, we showed that codend circumference and differences in hydrodynamic pressure had significant effects on the rates of movement of these fish through the square-mesh panel. The reaction of prawns to these stimuli was considered to be fairly limited, given their inability to maintain an escape response to trawls (see Lochhead, 1961; Main and Sangster, 1985).

In a recent experiment (Broadhurst and Kennelly, 1996) in one location in NSW, we tested a new design of codend, comprising composite panels of square-shaped mesh (referred to as the composite-panel codend), designed for and located in the codend, to take advantage of the theory discussed above. The results showed that this design was effective in reducing up to 40% of the total unwanted bycatch and up to 70% of the numbers of juveniles of commercially important species with no significant reduction in the catches of prawns and other commercially important species. Although not validated statistically, there was also some evidence to suggest that the trawls with the composite square-mesh panel retained, on average, slightly more prawns than a conventional trawl (means increased by up to 3%). This latter result, in particular, led numerous local fishermen to install the composite-panel voluntarily in their trawls and use it as part of normal commercial operations.

To assess the performance of this design throughout the full geographic range of this fishery (encompassing the range of fishing conditions and catches) and to promote its voluntary acceptance, our specific goals in the present study were to investigate the effectiveness of the composite-panel under normal commercial operations at four major ports along the NSW coast in 1) reducing unwanted bycatch, 2) maintaining catches of commercially important byproduct, and 3) increasing catches of prawns.

Materials and methods

This study was performed between December 1995 and February 1996 with four commercial vessels (see Table 1 for details) on prawn-trawl grounds offshore from four ports (Port Stephens, Southwest Rocks, Yamba, and Ballina) in New South Wales, Australia (Fig. 1). Each vessel was rigged with three Florida flyers (mesh size=42 mm) in a standard triple gear configuration (see Kennelly et al., 1993 for details), towed at 2.5 knots. Each of the identical outside nets on each vessel were rigged with zippers (no. 10 nylon open-ended auto-lock plastic slides) to facilitate removal and attachment of the codends. Because each of the middle nets were not rigged in exactly the same way as the outside nets, their catches were excluded from any analysis.

The codends used in the study measured 58 meshes long (2.3 m) and were constructed from 40-mm mesh

[2] Isaksen, B., and J. W. Valdemarsen. 1986. Selectivity experiments with square mesh codends in bottom trawl. Int. Coun. Explor. Sea council meeting 1986/B: 28, 18 p.

[3] Suuronen, P. 1990. Preliminary trials with a square mesh codend in herring trawls. Int. Coun. Explor. Sea, council meeting 1990/B: 28, 14 p.

Table 1

Summary of vessels, trawl headline lengths, and depths trawled for each of the four ports.

Port	Vessel and (length in m)		Trawl headline length for each net (m)	Depth trawled (m)
Port Stephens	*Fairwind*	(16)	16.45	75–88
Southwest Rocks	*Shelley-Anne*	(13.7)	10.97	47–53
Yamba	*L-Margo*	(15.93)	12.8	20–49
Ballina	*New Avalon*	(18.5)	14.63	29–55

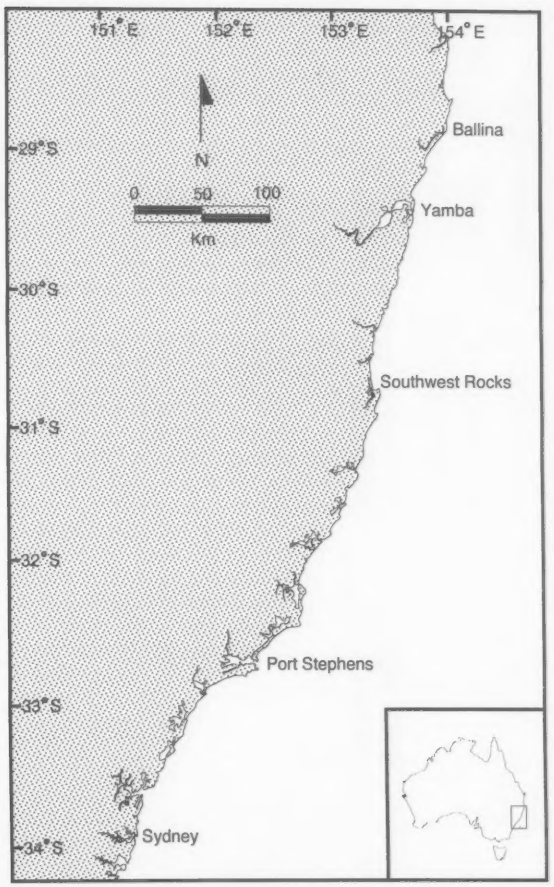

Figure 1

Map of New South Wales showing locations of the four ports that were sampled (Ballina, Yamba, Southwest Rocks, and Port Stephens).

netting and 48-ply twine (Fig. 2). They comprised two sections: the anterior section was 100 meshes in circumference, 33 meshes in length, and attached to a zipper; the posterior section was 150 meshes in circumference and 25 meshes in length. Two designs of codend were compared. The control codend was made entirely of diamond-shaped meshes (Fig. 2A). The second codend (termed the composite-panel codend) was similar to the control but had composite panels made of 60-mm and 40-mm netting cut on the bar and inserted into the top of the anterior section (Fig. 2B—see also Broadhurst and Kennelly, 1996). The composite-panel codend was designed so that the load was distributed anteriorly and laterally to the panel of 60-mm square-mesh, allowing this 60-mm panel to remain open. We predicted that 1) large numbers of fish would escape through this panel, located at the point where waterflow was thought to be greatest and that 2) in addition to reducing load on the 60-mm panel, the 40-mm square-mesh would also facilitate the escape of smaller fish.

The two codends were compared with each other in independent, paired trials, with the two outside nets of each vessel at each location. The codends were used in normal commercial tows of 90-min duration and alternated after each shot (to eliminate biases between different trawls and sides of the vessels). Because some significant effects of a delay in haulback (the period between slowing the vessel and engaging the winch to haul the trawl) were detected in a previous experiment (Broadhurst et al., 1996), all tows were performed with no delay in haulback. The location of each tow was randomly selected from the available prawn-trawl locations that were possible under the fishing conditions. During a period of four nights at locations offshore from each of the four ports, we completed a total of 16 replicate tows (i.e. four separate paired comparisons of 16 replicate tows each throughout the fishery).

After each tow, the two codends were emptied onto a partitioned tray. Prawns and all commercially important species larger than the minimum legal size (retained commercials) were separated. The remaining bycatch (termed "discarded by-catch") was then sorted. This included individuals of commercially important species that were smaller than the minimum legal size ("discarded commercials"). Data collected from each tow were as follows: the total weight of king prawns and a subsample (50 prawns from each codend) of their sizes (to the nearest 1-mm carapace length); the weight of the discarded bycatch; the weights, numbers, and sizes (to the nearest 0.5 cm) of retained and discarded commercial species; the weights and the numbers of the most commonly occurring noncommercial species; and the total numbers of discarded commercial species. Several species (commercial and noncommercial) were caught in sufficient numbers to enable meaningful comparisons (see Table 2).

Data at each port for all replicates that had sufficient numbers of each variable (defined as >2 individuals in at least 8 replicates) were analyzed with one-tailed, paired *t*-tests (i.e. four separate analyses). Because a previous experiment had shown that trawls with the composite-panel have the potential to retain more prawns than conventional trawls (Broadhurst and Kennelly, 1996), we tested the hypothesis that the composite-panel codend caught more prawns but less total bycatch than the control codend. Where analyses provided similar results for weights and numbers of taxa, only data about numbers were included in the figures to conserve space. Size frequencies of prawns, as well as discarded stout

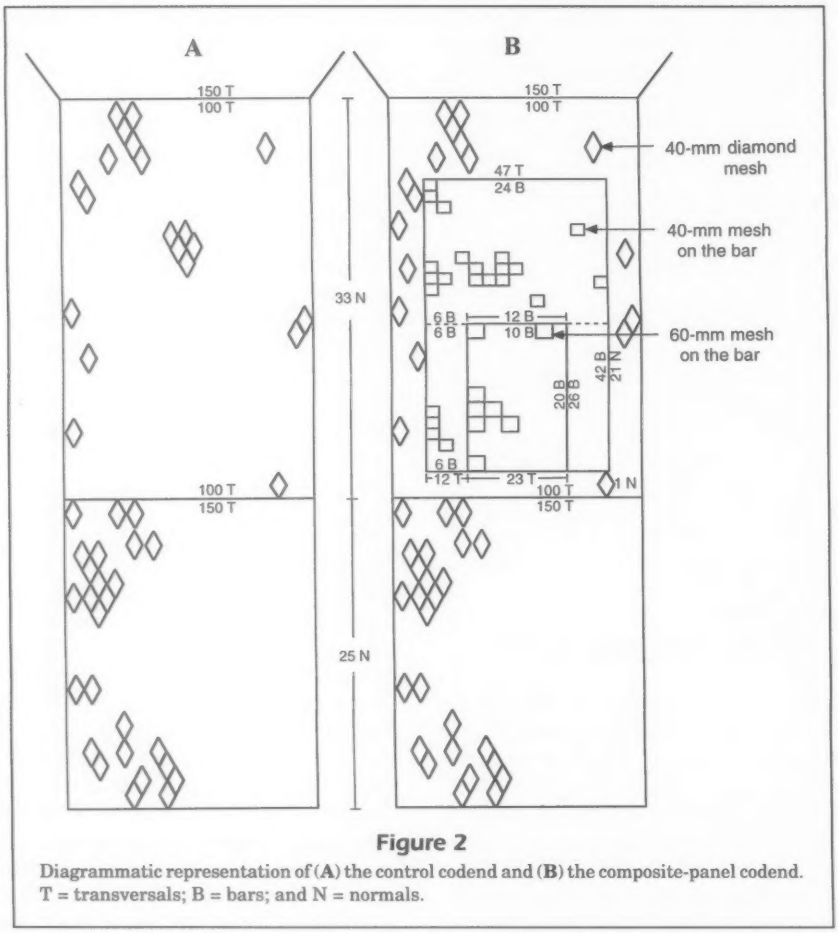

Figure 2

Diagrammatic representation of (**A**) the control codend and (**B**) the composite-panel codend. T = transversals; B = bars; and N = normals.

whiting, red spot whiting, and retained red mullet (where there were sufficient numbers) were plotted for each port and compared with two-sample Kolmogorov-Smirnov tests (P=0.05).

Results

Compared with the control codend, the composite-panel codend significantly reduced the weights of discarded bycatch (means reduced from 23.5% to 41%) at all four ports and significantly increased the catches of prawns at Port Stephens, Yamba, and Ballina (means increased by 14%, 5.5%, and 6%, respectively) (Fig. 3, A and B; Table 3). Although not to a significant degree (4%), the composite-panel codend used at Southwest Rocks also retained, on average, more prawns than the control codend (Fig. 3A). There were no significant reductions detected in the numbers and weights of commercial species retained by the composite-panel codend at any of the four ports (Fig. 3; Table 3).

The mean numbers and weights of discarded red spot whiting and stout whiting were reduced by the composite-panel codend at all locations where there were sufficient numbers to enable meaningful analysis (means reduced by up to 73%) (Fig. 3, F–G; Table 3). At Port Stephens, the composite-panel codend significantly reduced the numbers and weights of discarded john dory (by 50% and 57%, respectively) and blackeyes (by 45%) (Fig. 3, H and M; Table 3). There was a significant reduction in the numbers and weights of flutefish at Southwest Rocks (by 37% and 34%, respectively) and in the numbers and weights of red bigeye at Yamba (by 38.5% and 44%, respectively) and Ballina (by 35%) (Fig. 3, L and K; Table 3). There was also a significant reduction in the numbers and weights of leatherjacket (by 17% and 31%, respectively) and gurnard (by 41.5%) with the composite-panel codend at Ballina (Fig. 3, J and N; Table 3).

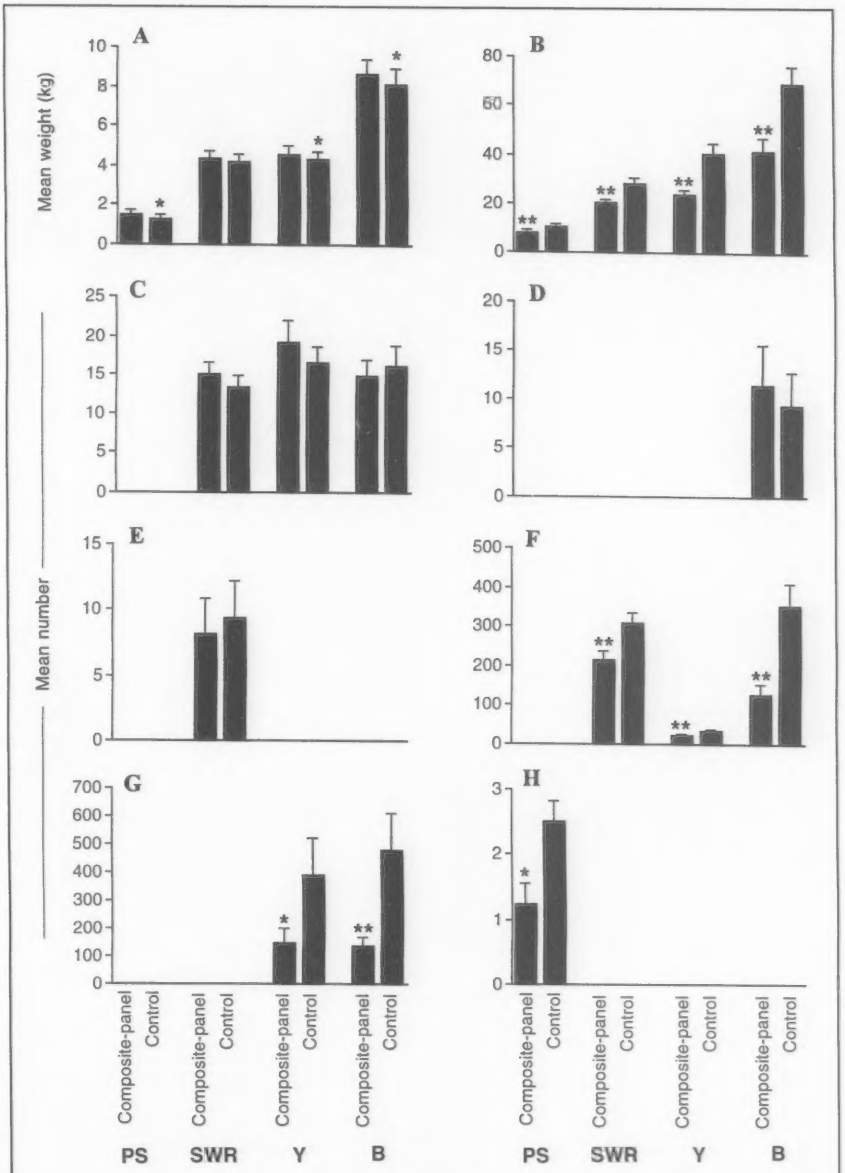

Figure 3

Differences in mean catches (± SE) between the control and composite-panel codends at each of the four ports: the weights of (**A**) prawns and (**B**) discarded bycatch; and the numbers of (**C**) retained octopus, (**D**) retained red mullet, (**E**) retained red spot whiting, (**F**) discarded red spot whiting, (**G**) discarded stout whiting, (**H**) discarded john dory, (**I**) discarded eastern blue spot flathead, (**J**) discarded leather jacket, (**K**) discarded red bigeye, (**L**) discarded flute fish, (**M**) discarded blackeyes, and (**N**) discarded gurnard. ** = significant ($P<0.01$); * = significant ($P<0.05$); PS = Port Stephens ; SWR = Southwest Rocks; Y = Yamba; and B = Ballina.

Two-sample Kolmogorov-Smirnov tests, comparing the size-frequency distributions for prawns, discarded red spot whiting, and retained red mullet measured from each sample at each site showed no differences in the relative size compositions of fish retained by the two codends (Figs. 4, 5, and 6C). There were no signifi-

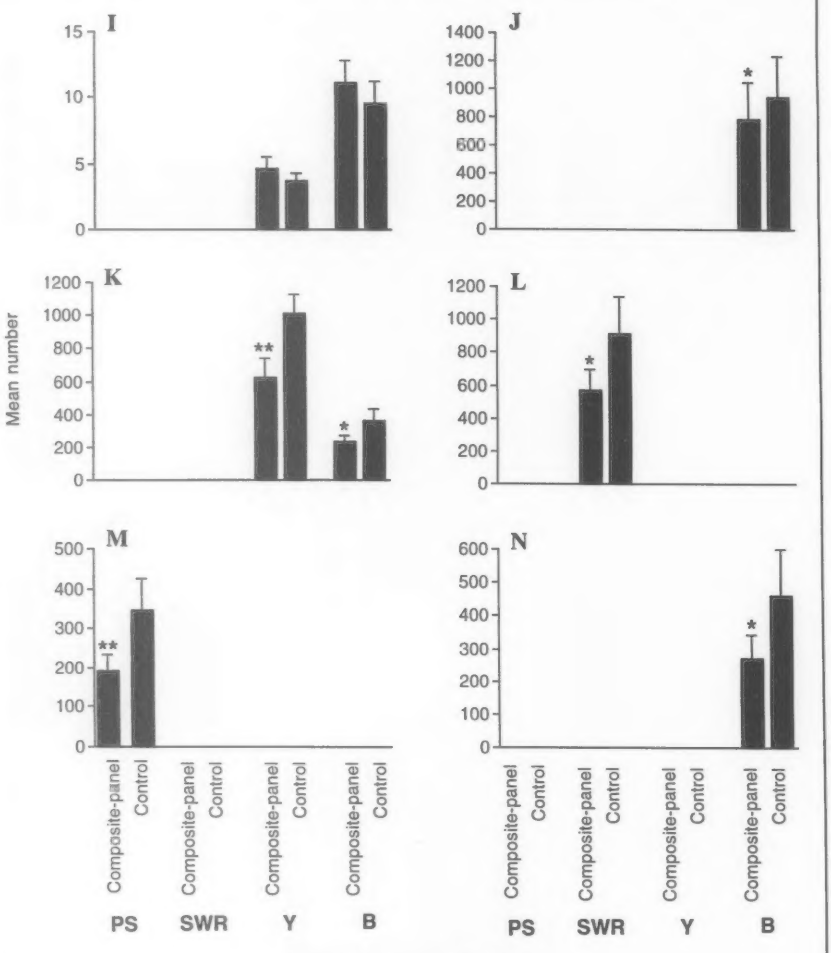

Figure 3 (continued)

Table 2
List of species caught in sufficient quantities to permit analyses.

Scientific name	Common name	Scientific name	Common name
Penaeus plebejus	eastern king prawn	*Platycephalus caeruleopunctatus*	eastern blue spot flathead
Octopus spp.	octopus	*Platycephalus richardsoni*	tiger flathead
Sepia spp.	cuttlefish	*Centroberyx affinis*	redfish
Sepioteuthis australia	southern calamary	*Paramonacantus filicauda*	threadfin leatherjacket[1]
Ibacus sp.	smooth bug	*Priacanthus macracanthus*	big redeye[1]
Pecten fumatus	scallop	*Macrorhamphosus scolopax*	flute fish[1]
Upeneichthys lineates	red mullet	*Apogonops anomalus*	blackeye[1]
Sillago flindersi	red spot whiting	*Lepidotrigla argus*	gurnard[1]
Sillago robusta	stout whiting		
Zeus faber	john dory		

[1] Denotes noncommercial species

Table 3

Summaries of one-tailed paired *t*-tests comparing the composite-panel and control codends. pt-v = paired *t*-value; *n* = number of replicates; all weights are in kilograms. disc = discarded; ret = retained; s. calamari = southern calamari; s. bug = smooth bug; rsw = red spot whiting ; sw = stout whiting; ebs = eastern bluespot flathead; and comm. sp. = commercial species. Significant *P*-values are in bold; insufficient data are marked by a dash.

	Port Stephens			Southwest Rocks			Yamba			Ballina		
	pt-v	*P*	*n*	pt-v	*P*	*n*	pt-v	*P*	*n*	pt-v	*P*	*n*
Wt of prawns	2.139	**0.024**	16	1.366	0.090	16	2.104	**0.026**	16	1.963	**0.034**	16
Wt of disc bycatch	4.467	**0.0002**	16	2.930	**0.0001**	16	5.518	**0.0001**	16	8.254	**0.0001**	16
No. of ret octopus	—	—	—	–0.913	0.812	16	–1.959	0.964	15	0.904	0.190	16
Wt of ret octopus	—	—	—	–0.868	0.800	16	–0.298	0.615	15	–0.341	0.631	16
No. of disc octopus	—	—	—	0.000	•	10	—	—	—	—	—	—
Wt of disc octopus	—	—	—	–0.171	0.566	10	—	—	—	—	—	—
No. of ret cuttlefish	—	—	—	–0.324	0.624	13	—	—	—	—	—	—
Wt of ret cuttlefish	—	—	—	–0.434	0.664	13	—	—	—	—	—	—
No. of disc cuttlefish	0.631	0.272	10	0.500	0.312	16	—	—	—	—	—	—
Wt of disc cuttlefish	0.165	0.436	10	0.995	0.167	16	—	—	—	—	—	—
No. of ret s. calamari	—	—	—	1.011	0.166	13	—	—	—	—	—	—
Wt of ret s. calamari	—	—	—	1.532	0.075	13	—	—	—	—	—	—
No. of disc s. calamari	—	—	—	0.703	0.248	12	—	—	—	—	—	—
Wt of disc s. calamari	—	—	—	0.887	0.197	12	—	—	—	—	—	—
No. of ret s. bug	0.452	0.329	13	—	—	—	—	—	—	—	—	—
Wt of ret s. bug	1.214	0.124	13	—	—	—	—	—	—	—	—	—
No. of disc s. bug	—	—	—	–0.254	0.597	8	–0.541	0.701	15	—	—	—
Wt of disc s. bug	—	—	—	0.344	0.371	8	–0.593	0.718	15	—	—	—
No. of disc scollop	—	—	—	–0.377	0.644	16	–1.109	0.542	9	—	—	—
Wt of disc scollop	—	—	—	0.501	0.312	16	0.348	0.368	9	—	—	—
No. of ret red mullet	—	—	—	—	—	—	—	—	—	–1.012	0.833	12
Wt of ret red mullet	—	—	—	—	—	—	—	—	—	–0.345	0.632	12
No. of ret rsw	—	—	—	0.893	0.194	14	—	—	—	—	—	—
Wt of ret rsw	—	—	—	1.270	0.113	14	—	—	—	—	—	—
No. of disc rsw	—	—	—	4.911	**0.0001**	16	3.593	**0.004**	8	3.704	**0.001**	15
Wt of disc rsw	—	—	—	4.574	**0.0002**	16	2.554	**0.019**	8	3.979	**0.0007**	15
No. of disc sw	—	—	—	—	—	—	2.776	**0.011**	10	2.958	**0.005**	16
Wt of disc sw	—	—	—	—	—	—	2.566	**0.015**	10	3.077	**0.004**	16
No. of disc john dory	2.611	**0.012**	12	—	—	—	—	—	—	—	—	—
Wt of disc john dory	3.174	**0.004**	12	—	—	—	—	—	—	—	—	—
No. of disc ebs	—	—	—	—	—	—	–1.139	0.862	14	–1.037	0.842	16
Wt of disc ebs	—	—	—	—	—	—	–0.919	0.812	14	–0.971	0.826	16
No. of ret tiger flathead	–0.349	0.634	13	—	—	—	—	—	—	—	—	—
Wt of ret tiger flathead	–0.602	0.721	13	—	—	—	—	—	—	—	—	—
No. of disc tiger flathead	1.282	0.111	14	—	—	—	—	—	—	—	—	—
Wt of disc tiger flathead	1.71	0.055	14	—	—	—	—	—	—	—	—	—
No. of disc redfish	0.947	0.179	15	—	—	—	—	—	—	—	—	—
Wt of disc redfish	–0.131	0.551	15	—	—	—	—	—	—	—	—	—
No. of leatherjacket	—	—	—	—	—	—	—	—	—	2.404	**0.014**	16
Wt of leather jacket	—	—	—	—	—	—	—	—	—	2.15	**0.024**	16
No. of red bigeye	—	—	—	—	—	—	3.344	**0.002**	16	2.528	**0.012**	15
Wt of red bigeye	—	—	—	—	—	—	4.122	**0.0004**	16	2.548	**0.012**	15
No. of flutefish	—	—	—	1.841	**0.045**	13	—	—	—	—	—	—
Wt of flutefish	—	—	—	1.851	**0.044**	13	—	—	—	—	—	—
No. of blackeyes	4.364	**0.0003**	16	—	—	—	—	—	—	—	—	—
Wt of blackeyes	5.459	**0.0001**	16	—	—	—	—	—	—	—	—	—
No. of gurnard	—	—	—	—	—	—	—	—	—	2.392	**0.018**	15
Wt of gurnard	—	—	—	—	—	—	—	—	—	2.034	**0.033**	15
No. of disc comm sp	1.168	0.1306	16	–2.282	0.981	16	0.436	0.334	16	–0.674	0.744	16

cant differences detected in the size-compositions of stout whiting at Yamba (Fig. 6A); however, at Ballina, the control codend caught proportionally more small stout whiting than the composite-panel codend (Fig. 6B).

Discussion

This study has shown the effectiveness of square-mesh panels in allowing nontarget organisms to es-

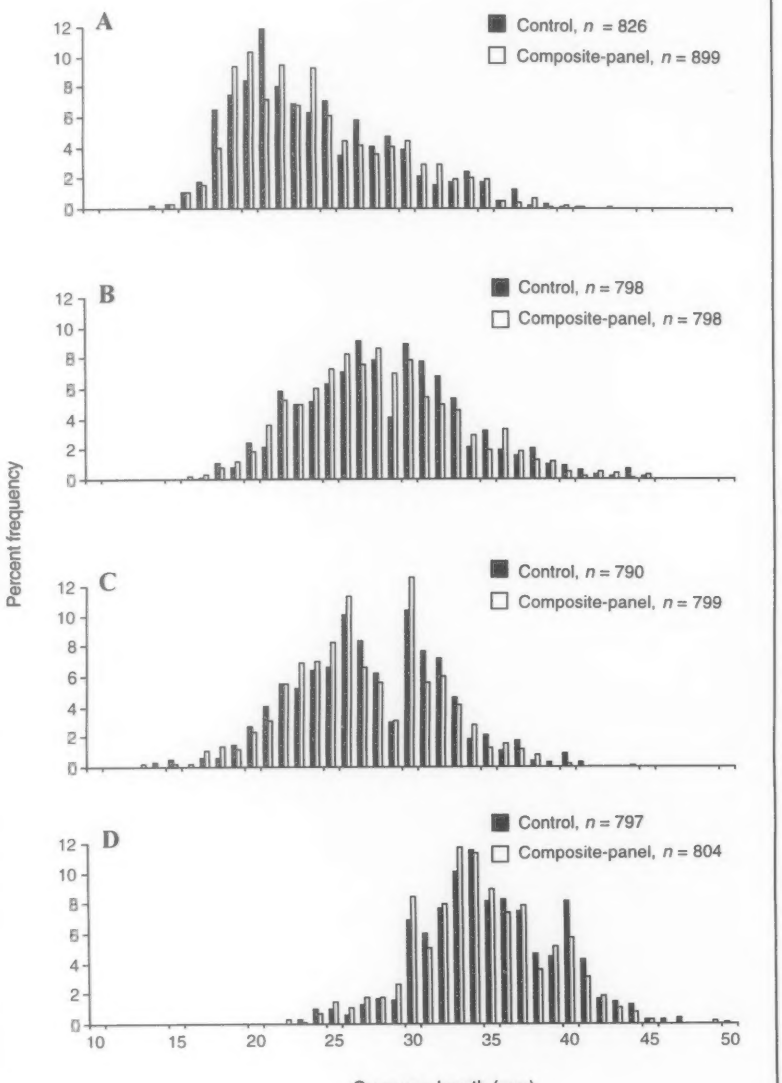

Figure 4

Size-frequency distributions of king prawns caught with control and composite-panel codends from (**A**) Port Stephens, (**B**) Southwest Rocks, (**C**) Yamba, and (**D**) Ballina.

cape trawls (see also Briggs, 1992; Fonteyne and M'Rabet, 1992; Broadhurst and Kennelly, 1994, 1995, 1996; Broadhurst et al., 1996) while maintaining catches of commercially important species. By conducting independent experiments on different vessels across four ports over a range of fishing conditions and catches, we have also provided information on the relative performance of the composite-panel throughout the full operational range of the NSW oceanic prawn-trawl fishery and have documented, for the first time, a significant increase in the catch of targeted prawns with this design.

The composite-panel codend was most effective in excluding large quantities of those discarded species that are relatively fusiform and of a size small enough to pass through the square-meshes. Species such as

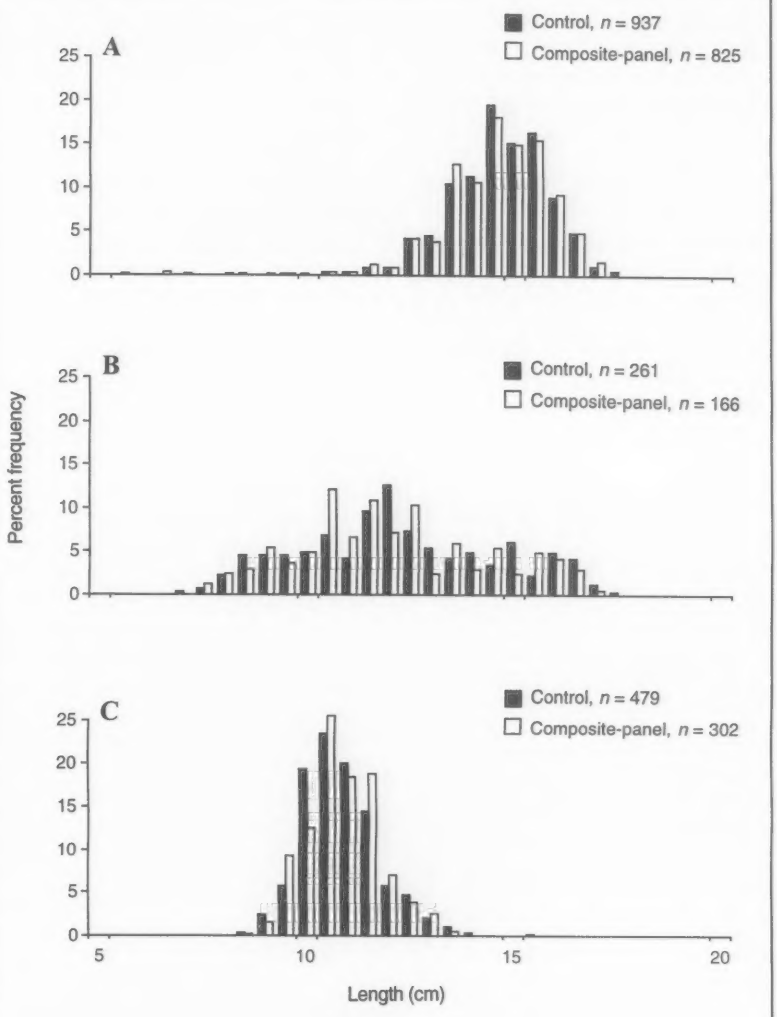

Figure 5

Size-frequency distributions of discarded red spot whiting caught with control and composite-panel codends from (**A**) Southwest rocks, (**B**) Yamba, and (**C**) Ballina.

blackeyes, flute fish, red bigeye, and, in particular, stout and red spot whiting, were all significantly reduced by the composite-panel, which contributed towards a reduction in the mean weight of discarded bycatch at all locations from 23.5% to 41% (Fig. 3). Assuming minimal differences between the various vessels and their gear, the relative availability of these fusiform species throughout waters off New South Wales may explain the variations in the mean reductions of total discarded bycatch at each of the ports and across the fishery. For example, there were no red spot or stout whiting captured at Port Stephens (Fig. 3, E–G), and there was only a 23.5% reduction in total discarded bycatch by the composite-panel at that location (Fig. 3B). In contrast, the discarded bycatch at Yamba and Ballina included large numbers of whiting and red bigeye (up to 500 fish and 1,000 fish, respectively, from each tow in the control net) (Fig. 3, E–F and K) and correspondingly large percentage reductions in total discarded bycatch (41% and 39.5%, respectively) (Fig. 3B).

The above reductions in total discarded bycatch with the composite-panel provide a possible explanation for the significant increase in catches of

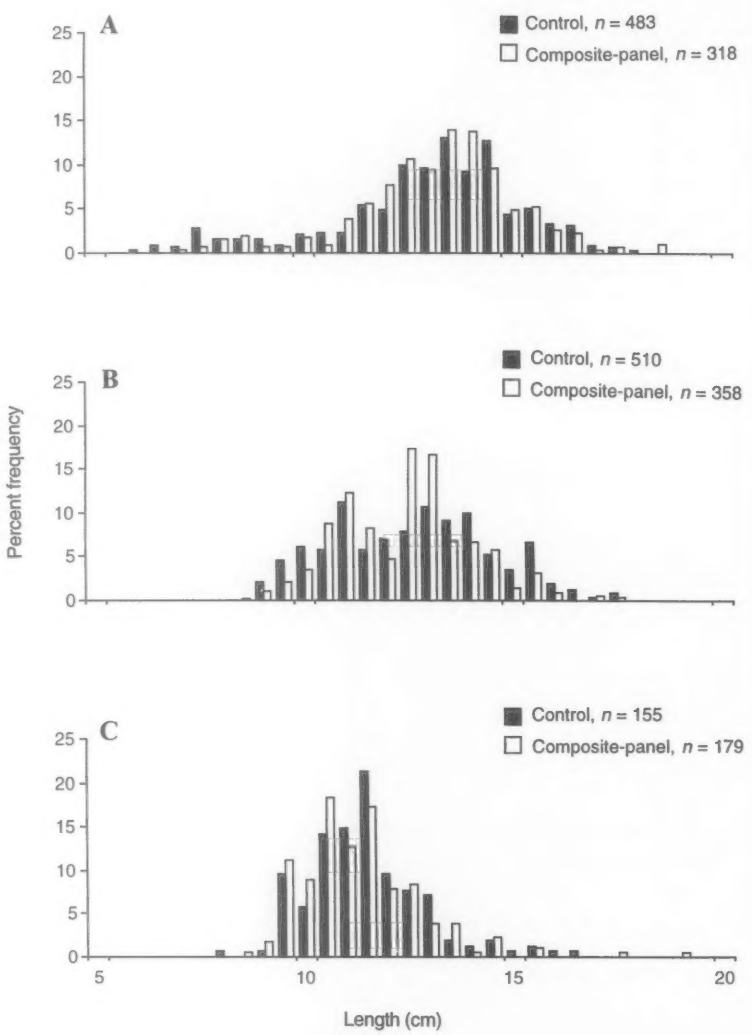

Figure 6

Size-frequency distributions of discarded stout whiting caught with control and composite-panel codends from (**A**) Yamba, (**B**) Ballina, and (**C**) size-frequency distributions of retained red mullet from Ballina.

prawns at Port Stephens, Yamba, and Ballina (by 14%, 5.5%, and 6%, respectively) and for the nonsignificant increase of 4% at Southwest Rocks (Fig. 3A). By reducing the amount of total discarded bycatch and therefore the weight and drag in the codend, the trawl with the composite-panel may have achieved greater spreads between the otter boards (i.e. an increased swept area) than did the control, thereby covering more of the seabed and capturing more prawns. These prawns were probably the same sizes as those that we sampled, because Kolmogorov-Smirnov tests failed to detect any significant differences in prawn sizes between the codends for any of the ports (Fig. 4).

In support of the theory discussed above, there was also an increase (although not statistically significant) in the mean numbers of retained octopus at Southwest Rocks and Yamba (by 11% and 14%, respectively), retained red mullet (by 17%) at Ballina, and discarded eastern blue spot flathead at Yamba and Ballina (by 19.5% and 14.5%, respectively) with the composite-panel (Fig. 3, C–D, and I; Table 1).

Given the physical profile of these individuals and their large size, it is unlikely that once captured by the trawl, they would have been able to fit through the small square-meshes of the composite-panel. In a previous study (Broadhurst and Kennelly, 1996), we showed that large quantities of small individuals of long spined flathead, *Platycephalus longispinis*, escaped through the square-meshes in the composite-panel (62% reduction compared with a conventional codend). Because the tiger and eastern blue spot flathead captured in the present study are physically similar to this species, it may be possible to facilitate their escape simply by increasing the size of mesh in the panel (assuming they display similar responses to stimuli from the trawl). Such a modification, however, would likely result in less retention of smaller individuals of commercially important species such as red spot and stout whiting (see Figs. 5 and 6, A–B), cuttlefish, and southern calamari. In addition, the composite-panel has been designed so that the load is distributed across the many bars of the 40-mm square-shaped mesh. Any major increase in this mesh size would result in the distribution of load across fewer bars, possibly altering the geometry of the codend and its overall performance.

In the present study, we have shown that the composite-panel codend consistently increased catches of prawns over a range of operational conditions while removing large quantities of unwanted bycatch throughout the entire geographic range of the NSW oceanic prawn-trawl fishery. In another study in Australia, Robins-Troeger et al. (1995) tested a large and comparatively complex BRD (termed the "AusTED") off northern Australia and, despite reports of significant losses of prawns, concluded that "the AusTED system has the potential to be developed to suit trawling conditions encountered in different Australian prawn fisheries." It is unlikely, however, that any design of a BRD would be accepted and endorsed by fishermen if it did not consistently maintain catches of the target species throughout the range of the fishery—as is shown to be the case in the present paper for the composite-panel codend (see also Kendall, 1990; Renaud et al., 1992).

In terms of promoting a large-scale voluntary adoption of BRD's, like the composite-panel described in the present paper, it is useful to provide industry not only with evidence of catch rates similar to those obtained with conventional gear but also with evidence of additional benefits, such as a potential for increasing duration of tows, improving quality of catches (due to less damage from bycatch in the codend), increasing savings in labor and fuel, reducing sorting times, and reducing conflicts with other user groups (e.g. recreational and commercial fishermen targeting stocks of bycatch species). The realization of these incentives, along with the results from the present study, have resulted in many commercial fishermen using the composite-panel throughout the entire NSW oceanic prawn-trawl fishery.

Acknowledgments

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Movements, feeding periods, and daily ration of piscivorous young-of-the-year bluefish, *Pomatomus saltatrix*, in the Hudson River estuary*

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Abstract.—Young-of-the-year (YOY) bluefish, *Pomatomus saltatrix*, were collected during the summers of 1992 and 1993 in the Hudson River estuary with beach seine, surface trawl, and gill nets. The temporal and spatial patterns of catch-per-unit-of-effort (CPUE) and gut-fullness values were used to infer bluefish movement and feeding periods, respectively. Estimates of daily ration were made from gut-fullness values and previously published estimates of gastric evacuation rate. Nearshore beach-seine CPUE was highest during day collections and lowest at night. Offshore gill-net CPUE was highest during crepuscular or night periods and lowest during day sets. Hence, YOY bluefish appear to occupy nearshore environments during the day and move away from shore at night. Gut-fullness values for bluefish captured with beach seines were highest at diurnal and crepuscular periods and declined at night; however, there were indications of night feeding on some dates. The magnitude and pattern of daily ration estimates of YOY bluefish in the Hudson River estuary were similar to values measured in previous studies with other methods. Interannual differences in the magnitude of daily ration were observed and may be a result of day-to-day variation in feeding or differences in available prey type and size. Clupeids, striped bass, and bay anchovy were important prey in 1992, whereas striped bass, bay anchovy, and Atlantic silversides were the dominant prey of YOY bluefish in 1993. Improved understanding of the spatial and temporal patterns of bluefish feeding, as well as fine-scale temporal resolution of estimates of bluefish consumption rates, will aid in assessing the impact of YOY bluefish predation on fish populations within the Hudson River estuary.

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The movements of fishes are controlled by both biotic and abiotic phenomena. In estuaries, fish may move in relation to the availability of prey and to reduce the risk of predation, as well as in response to fluctuations in light, tide, salinity, temperature, and dissolved oxygen levels (Miller and Dunn, 1980). Fish distribution is often controlled by the interacting effects of these factors (Miller and Dunn, 1980; Gibson et al., 1996). An understanding of the factors that govern the movements and distributions of predators and prey is prerequisite to quantifying predator-prey interactions.

The bluefish, *Pomatomus saltatrix*, is a marine piscivorous predator of circumglobal distribution. On the U.S. east coast, spawning occurs offshore over the continental shelf, but young-of-the-year (YOY) migrate abruptly into estuaries at ~60 mm fork length (Kendall and Walford, 1979; Nyman and Conover, 1988; McBride and Conover, 1991; Juanes and Conover, 1995). Bluefish spawned in the South Atlantic Bight in the spring (spring-spawned) are advected northward in waters associated with the Gulf Stream (Hare and Cowen, 1996) and move into New York-New Jersey estuaries in June (Nyman and Conover, 1988; McBride and Conover, 1991). A second wave of recruits made up of summer-spawned fish (spawned in the Middle Atlantic Bight) appear in nearshore waters in mid- to late-summer. The habitat shift from oceanic waters to estuarine areas coincides with a shift from feeding that is zooplanktivorous to one that is piscivorous (Marks and Conover, 1993).

This study is part of a larger project designed to estimate the predatory impact that YOY bluefish have on their piscine prey populations in the Hudson River estuary. Young-of-the-year bluefish are known to prey on larval and juvenile fishes in marine embayments and estuaries along the U.S. east coast (Grant, 1962; Friedland et al., 1988; Juanes et al., 1993; Creaser and Perkins, 1994; Hartman and Brandt, 1995a; Juanes and Conover, 1995). In the Hudson River estuary, YOY bluefish prey include the young of several resource species such as striped bass, *Morone sax-*

* Contribution 1067 of the Marine Sciences Research Center, State University of New York, Stony Brook.

atilis, and American shad, *Alosa sapidissima* (Juanes et al., 1993; 1994). Mortality caused by YOY bluefish predation may be intense given the relatively high consumption rates of this species (Juanes and Conover, 1994; Buckel et al., 1995). In order to assess the effect of YOY bluefish predation, an understanding of the location and timing of bluefish prey interactions, as well as accurate and fine-scale temporal measurements of bluefish consumption rates, are needed.

Consumption rates of fish are measured with direct methods (laboratory- or field-based) and indirect methods. The field-based method requires measurements of gut fullness over a diel cycle coupled with estimates of gastric evacuation rate (Elliott and Persson, 1978; Eggers, 1979). The indirect method most widely used is a bioenergetic approach that requires knowledge of the predator's growth trajectory, physiological parameters, and environmental data (Kitchell et al., 1977). Because all of these methods have their drawbacks and their use is controversial (Hewett et al., 1991; Boisclair and Leggett, 1991), we used a combination of different techniques in order to compare methods and cross-validate results.

Juanes and Conover (1994) and Buckel et al. (1995) measured YOY bluefish consumption rates in the laboratory. Steinberg (1994) estimated daily ration of Hudson River YOY bluefish with a bioenergetics modeling approach. However, the only two field estimates of bluefish consumption rates that exist were made in Great South Bay, NY (Juanes and Conover, 1994), an environment that differs from the Hudson River estuary.

Here we report on the results of diel field collections of YOY bluefish during the summers of 1992 and 1993 in the Hudson River estuary. These collections allowed us to determine temporal and spatial (e.g. inshore vs. offshore) patterns of YOY bluefish movements and feeding. Gut-fullness values were coupled with previously determined estimates of gastric evacuation rates (Buckel and Conover, 1996) to estimate YOY bluefish daily ration.

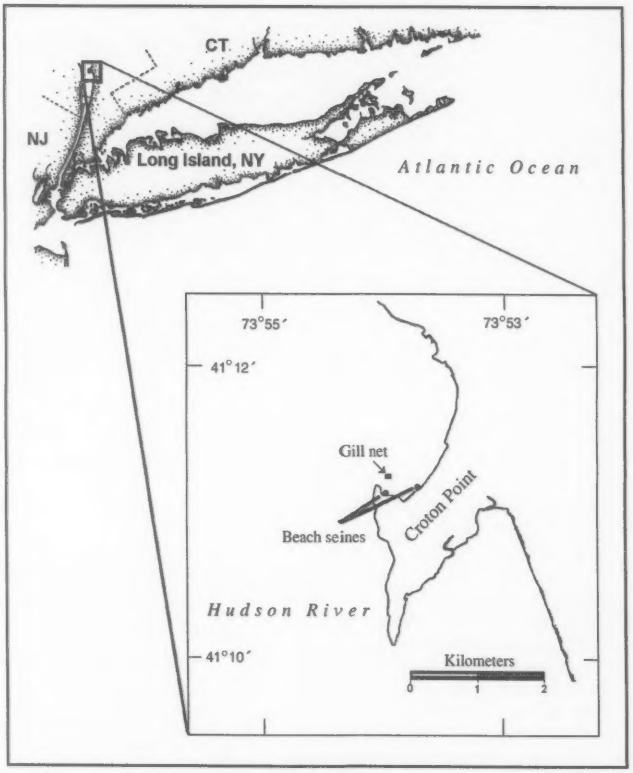

Figure 1

Locations where beach seines and gill nets were used at Croton Point, New York, in the lower Hudson River estuary.

Methods

Diel collections—beach seine

Spring- and summer-spawned YOY bluefish (cohorts easily identified by size) and their prey were collected from the lower Hudson River estuary in 1992 and 1993 on the north shore of Croton Point (41°11'N, 73°54'W; Fig. 1). Ten diel beach-seine collections were made: five in 1992 (16–17 July, 28–29 July, 13–14 August, 26–27 August, and 19–20 September) and five in 1993 (7–8 July, 20–21 July, 4–5 August, 18–19 August, and 11–12 September). Collections were made every three hours beginning at 1200 h and ending at 1200 h the following day. Sampling began 30 min before and ended 30 min after each time point (e.g. sampling for the 1200 time point began at 1130 and ended at 1230). A 60 × 3 m beach seine (13-mm-mesh wings, 6-mm-mesh bag) and a 30 × 2 m beach seine (6-mm-mesh wings, 3-mm-mesh bag) were used for nearshore sampling. The 60-m seine was set by boat. A minimum of two 60-m seine hauls were made during each one-hour sampling period. Additional seine hauls were sometimes made to increase bluefish sample size. Bluefish and samples of prey were immediately preserved in 10% formalin. Catch-per-unit-of-effort (CPUE) of bluefish was calculated as the number of fish caught per seine haul in the first two 60-m seine hauls. Potential prey were counted

from one haul of each of the 60- and 30-m seines in 1993. Temperature (thermometer), salinity (refractometer), and dissolved oxygen (modified Winkler's method) were measured at each time point. Periodic functions were used to obtain quantitative values of tide and light levels for statistical analyses. Tides at the study site are semidiurnal and the tidal amplitude is ~1.5 m. The state of tide (T) for any given time point was calculated from the following equation:

$$T = \cos\left(\left((2\pi / 12.42) \times \text{time of day}\right) - \theta\right),$$

where θ = the time of high tide in radians.

A value for illumination (watts/cm^2) was calculated for each time point on each specific date (Kuo-Nan, 1980).

The effects of light, tide, salinity, dissolved oxygen, and temperature on CPUE of spring-spawned bluefish were examined with a forward step-wise multiple regression. Data from 1992 and 1993 were analyzed separately and $\log_e (x+1)$ transformed to remove heterogeneity of variances.

Diel collections—gill net and surface trawl

A 90 × 2 m (4-cm-stretch, 2-cm-square) monofilament surface gill net was used to collect spring-spawned YOY bluefish from offshore shoal areas. One end of the gill net was anchored approximately 30 m east of the northernmost tip of Croton Point at a depth of ~3 m (low tide) and set parallel to the north shore of Croton Point (see Fig. 1). The nearest beach-seine site was ~200 m away in the cove just south of the gill-net set location. Gill-net collections were made concurrently with diel beach-seine collections on 20–21 July (approximate mid-set times were 1500, 2100, 0600), 4–5 August (2100, 0130, 0600), and 18–19 August (1500, 2100, 0130, 0600) in 1993. Soak times always lasted two hours. After net retrieval, bluefish were removed and immediately frozen on dry ice. Fish from gill-net collections were not used in the calculation of daily ration. Relative abundances of bluefish were calculated as the number of fish caught per hour of soak time (CPUE).

A surface trawl collection (8.2-m head-rope, 6.7-m foot-rope, 0.9-m-opening height, 2.5-cm-mesh net, 0.6-cm-mesh codend) towed between two boats was made on 15–16 July 1993. It was conducted 1) to supplement night beach-seine collections, 2) to determine YOY bluefish movement patterns, and 3) to estimate daily ration. Collections were made every three hours beginning at 1230 and ending at 1230 the following day. Two to three ten-minute tows were made at each time point. Tow speed was approximately 4 knots. Bluefish and prey were immediately preserved in 10% formalin. Relative abundances of bluefish were calculated as the number of fish caught per trawl (CPUE).

Diel collections—"movement collection"

A combination gill-net and beach-seine collection was made on 11–12 August 1993 with the sole purpose of examining bluefish movement at crepuscular periods. Fish from these collections were not used in the calculation of daily ration. Collections with beach seines were performed at 1200, 2400, and one hour before and after sunrise (0520 and 0720) and sunset (1900 and 2100). The temporal resolution of this sampling scheme with respect to sunrise and sunset was higher than that of evenly spaced intervals of beach seining described above (every three hours). Gill-net collections lasted two hours and were made throughout the diel cycle.

Feeding period

Values of gut fullness were used to examine the feeding periods of beach-seine-collected YOY bluefish. Gut-fullness values (F) were calculated as

$$F = G/W,$$

where G = prey wet weight; and
W = bluefish wet weight (total weight minus prey wet weight; see "Diet analysis" below).

Arc-sin square root and $\log_e (x+1)$ transformations of individual gut-fullness values did not remove heteroscedasticity; therefore, the effect of time on gut-fullness values from beach-seine data (excluding 11–12 Aug and 11–12 Sep 1993) was examined with a nonparametric Kruskal-Wallis ANOVA. If treatment effects were significant, a nonparametric multiple comparison test for unequal sample sizes (Zar, 1984) was used to compare means.

Daily ration estimates

Values of gut fullness for spring-spawned bluefish from beach-seine (five dates in 1992 and four dates in 1993) and surface trawl (15–16 July 1993) collections were used in estimating daily ration. Daily ration was also estimated for summer-spawned bluefish captured during beach-seine collections (19–20 Sept. 1992). The Elliott and Persson (1978) food consumption model was used to estimate bluefish daily ration:

$$C_{\Delta t} = \frac{(\overline{F}_{t_2} - \overline{F}_{t_1} \cdot e^{-R_e t}) \cdot R_e t}{1 - e^{R_e t}}$$

where $C_{\Delta t}$ = food consumption between sampling periods at time t_2 and t_1;
$\overline{F}_{t_2}$ and $\overline{F}_{t_1}$ = the geometric mean gut-fullness values (back-transformed from $\log_e (x+1)$) at these time points (time points with $n < 3$ fish were not used in daily ration calculation);
R_e = the exponential gastric evacuation rate; and
$t = t_2 - t_1$.

Daily ration was calculated by summing estimates of $C_{\Delta t}$.

The method of Boisclair and Marchand (1993) and Trudel and Boisclair (1993) was used to estimate 95% confidence intervals for daily ration estimates. There were four steps in the analysis. First, an estimate of exponential evacuation rate (R_e) was made from the average water temperature during a given sampling period. Estimates of R_e were calculated from the equation

$$R_e = 0.015e^{(0.103T)},$$

where T = water temperature (°C) from Buckel and Conover (1996).

Periods of declining gut fullness can be used as a validation of laboratory-based gastric evacuation rates (see Parrish and Margraf, 1990) and were used for seven out of ten diel beach-seine collections with the same data analysis techniques as those described in Buckel and Conover (1996). The mean field-derived estimate of R_e for these dates was 0.241/h, and the laboratory-derived estimate was 0.201/h (± 0.038 SE).

Second, a normal distribution of 1,000 pseudo values of R_e were calculated as

$$R_e^* = R_e + (SE_{Re} \times RN),$$

where R_e^* = the pseudo value of evacuation rate;
R_e = the estimated mean evacuation rate;
SE_{Re} = the standard error of R_e (Buckel and Conover 1996); and
RN = a random number (different for each calculation) from a normal distribution with a mean of 0 and standard deviation of 1.

Third, a normal distribution of 1,000 pseudo values of gut fullness (F) were calculated for each time point as

$$F_t^* = F_t + (\mathrm{SE}_{Ft} \times RN),$$

where F_t^* = the pseudo value of gut fullness;
F_t = the mean $\log_e(F+1)$ transformed gut fullness;
SE_{Ft} = the standard error of F_t; and
RN = a random number (different for each calculation) from a normal distribution with a mean of 0 and standard deviation of 1.

Fourth, Monte-Carlo simulations were used to estimate $C_{\Delta t}$ from the above equations by randomly choosing values of R_e^*, $F_{t_1}^*$, and $F_{t_2}^*$ from the distributions of 1,000 pseudo values (values of $F_{t_1}^*$ and $F_{t_2}^*$ were back-transformed before calculation of $C_{\Delta t}$). Simulated values of $C_{\Delta t}$ were generated for each of the eight time intervals (nine sampling points; less if a time point had $n<3$ fish) and summed to estimate a daily ration. This calculation was repeated 1,000 times. The 2.5 and 97.5 percentiles of these daily ration estimates were taken as the 95% confidence intervals.

Diet analysis

Diets of bluefish captured with beach seines, surface trawls, and gill nets were quantified. In the laboratory, bluefish were measured for total length (TL, ± 1.0 mm), weighed (± 0.01 g), and their stomachs were extracted. Stomach contents of bluefish were identified to the lowest possible taxon, enumerated, blotted dry, weighed (± 0.01 g), and measured (TL, ± 1.0 mm; eye diameter, ± 0.1 mm; caudal peduncle depth, ± 0.1 mm). Regressions relating prey eye-diameter and caudal peduncle depth to TL were used to estimate prey TL from prey pieces (see Scharf et al., 1997). A reference collection of Hudson River fish species (whole fish, scales, and bones) was used to aid in identification of digested prey. Two indices were computed to describe diets (see Hyslop, 1980). The indices were 1) number of stomachs in which a taxon was found, expressed as a percentage of the total number of stomachs containing food (%F=percent frequency of occurrence), and 2) weight of taxon, expressed as a percentage of the total weight of food items (%W=percent weight).

Results

Diel collections—beach seine

A total of 1,204 spring-spawned and 64 summer-spawned bluefish were collected during diel beach-seine collections. There were five successful diel col-

lections in 1992 (571 spring- and 64 summer-spawned) and four in 1993 (633 spring-spawned fish). The sample size of bluefish from the 11–12 September 1993 beach-seine collection was too small (n=23) for all analyses except diet.

In the forward stepwise multiple-regression analysis, illumination of the surface waters was the only factor that explained a significant amount of the variation in spring-spawned bluefish CPUE for both 1992 (P=0.006) and 1993 (P<0.001). The influence of illumination on CPUE of spring-spawned bluefish was positive in both 1992 and 1993 (Fig. 2, A and B): more bluefish were captured by day than by night but daytime CPUE was more variable. The CPUE pattern was also seen with summer-spawned bluefish (Fig. 2A).

The number of prey captured in the 60- and 30-m seine hauls at each time point ranged from 1 to 1,910 in 1993. On three out of the four dates examined, the relation between numbers of prey and bluefish (from identical seine hauls) was positive; however, none of these correlations were significant.

Diel collections—gill net and surface trawl

A total of 154 bluefish were captured in gill-net sets on three diel collections in 1993. Mean CPUE was highest during sunset and midnight collections and lowest during afternoon and sunrise sets (Fig. 2C). A total of 94 bluefish were captured during surface trawl collections on 15–16 July 1993. Bluefish surface trawl CPUE was highest during the day (1500) and lowest at sunset (2100)(Fig. 2D).

Diel collections—"movement collection"

Gill nets and beach seines captured 29 and 47 bluefish on 11–12 August 1993, respectively. Gill-net CPUE was low during midday, increased through the evening to a peak at midnight (Fig. 2E), and then declined to zero by morning. Beach-seine CPUE was high during the day and low at night: the drop and increase in CPUE corresponded with sunset and sunrise, respectively.

Feeding period

Time of collection had a highly significant (Kruskal-Wallis ANOVA, P<0.001) effect on the gut-fullness values of spring-spawned bluefish in 1992 and 1993 (Figs. 3, A–F, and 4, A–E). Mean gut-fullness patterns from seine-collected bluefish in 1992 increased throughout the afternoon, peaked in late afternoon or evening, decreased throughout the night, and increased during the morning hours (Fig. 3A).

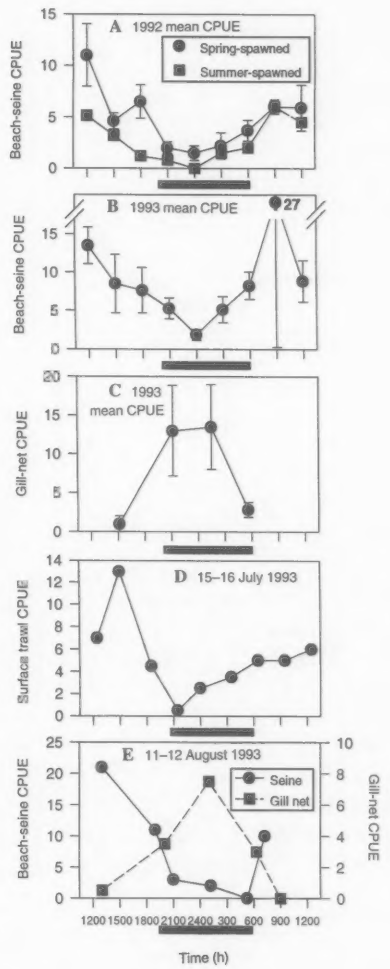

Figure 2

Catch-per-unit-of-effort (CPUE) of bluefish, *Pomatomus saltatrix*, versus time of capture during 1992 and 1993 diel collections. (**A**) Mean 1992 beach-seine CPUE (circles; ± SE) of spring-spawned bluefish averaged over all dates of collection (16–17 July, 28–29 July, 13–14 August, 26–27 August, and 19–20 September) and summer-spawned bluefish CPUE (squares) on 19–20 September. (**B**) Mean 1993 beach-seine CPUE (± SE) of spring-spawned bluefish averaged over all dates of collection (7–8 July, 20–21 July, 4–5 August, and 18–19 August). (**C**) Mean 1993 gill-net CPUE averaged over all dates of collection (20–21 July, 4–5 August, and 18–19 August). (**D**) Surface trawl CPUE on 15–16 July 1993. (**E**) CPUE of spring-spawned bluefish during the beach-seine (circles, solid line) and gill-net (squares, broken line) "movement collection" on 11–12 August 1993. The time periods from sunset to sunrise are indicated by dark horizontal bars.

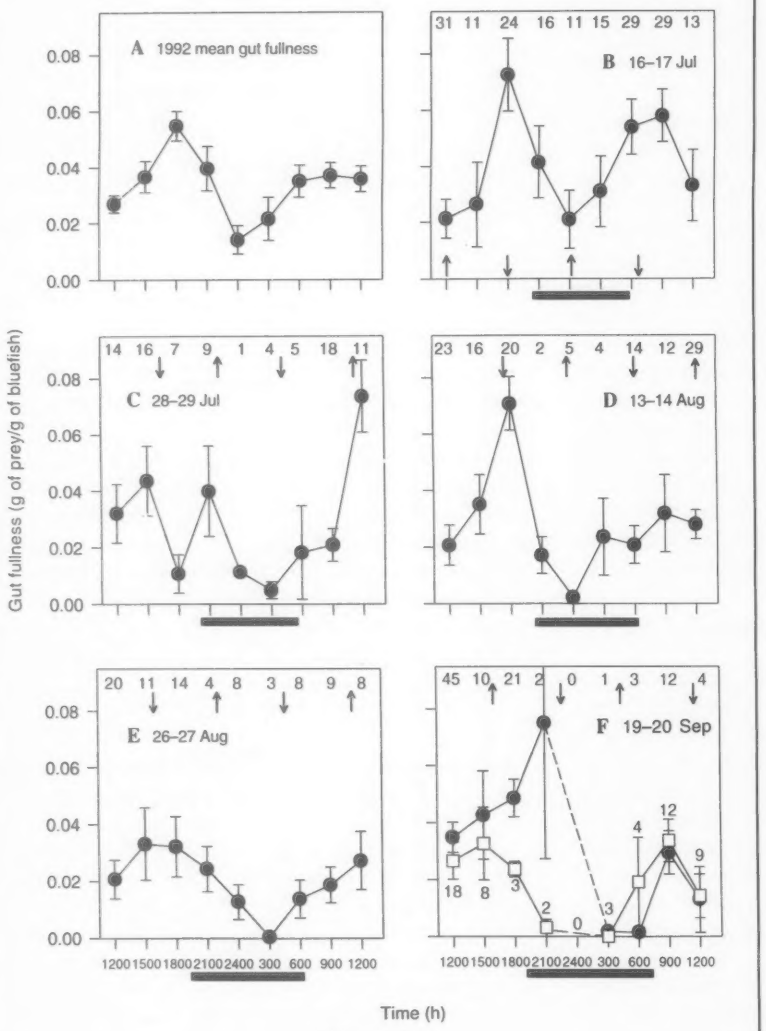
A 1992 mean gut fullness
B 16–17 Jul
C 28–29 Jul
D 13–14 Aug
E 26–27 Aug
F 19–20 Sep
Gut fullness (g of prey/g of bluefish)
Time (h)
1200 1500 1800 2100 2400 300 600 900 1200

Figure 3

Gut-fullness values (mean ± SE) of spring-spawned bluefish, *Pomatomus saltatrix*, versus time of capture during 1992 diel beach-seine collections. (**A**) Mean gut fullness (± SE) averaged across all dates of collection: (**B**) 16–17 July, (**C**) 28–29 July, (**D**) 13–14 August, (**E**) 26–27 August, and (**F**) spring-spawned (closed circles) and summer-spawned (open squares) bluefish versus time of capture during diel beach-seine collections on 19–20 September. The time periods from sunset to sunrise are indicated by dark horizontal bars. Numbers above (or near, for summer-spawned) each gut-fullness estimate represent bluefish sample size. Upward and downward facing arrows represent the time of high and low tide, respectively.

One potential problem in the above analysis is the potential lack of independence of gut-fullness estimates between time points. This lack of independence is mainly a concern with adjacent time points (spaced 3 hours apart) because gastric evacuation in bluefish is ~6–8 hours (Juanes and Conover, 1994; Buckel and Conover, 1996). Therefore, gut-fullness estimates at time points that are separated by at least six hours are more likely to be independent of each other. We used post-hoc comparisons to examine for statistical differences between such pairs.

The gut-fullness value at 1800 was significantly higher (nonparametric multiple-comparison test, $P<0.001$) than the gut-fullness value at 1200, 2400, and 0300. A similar pattern was seen for summer-spawned fish (Fig. 3F). The gut-fullness values of 1993 beach-seine-collected bluefish differed from those seen in 1992 (Fig. 4A); decline in gut fullness at night was not as dramatic. Gut-fullness values at 1200 were significantly lower ($P<0.01$) than values from morning (0600 and 0900) and evening (2100) collections. However, the lowest night gut-fullness value (0300) was not significantly different from the highest day (0600) gut-fullness value ($P>0.05$).

Daily ration estimates

Daily ration estimates for YOY spring-spawned bluefish during 1992 beach-seine collections were highest on our first sampling date 16–17 July at 22.2% body weight/d (95% confidence interval (CI) 13.3–32.3) and dropped to 7.3% body weight/d (1.7–13.6) by 19–20 September (Fig. 5A). Although there was a decline in daily ration, these values had overlapping CI's and were therefore not statistically different. In 1993, daily ration values from beach-seine-captured spring-spawned bluefish were highest on 20–21 July at 14.7% body weight/d (8.5–21.6) and lowest on 7–8 July at 10.1% body weight/d (6.7–14.0) (Fig. 5B). The diel collection made with surface trawls on 15–16 July 1993 yielded a daily ration estimate of 8.6% body weight/d (4.7–12.8).

Estimates of daily ration in 1993 were not statistically different from each other. Daily ration of summer-spawned fish on 19–20 September 1992 was 5.7% body weight/d (2.6–9.4).

Diet analysis

Diets of YOY bluefish collected with beach seines during 1992 and 1993 were dominated by fish. Fish prey represented 97–100% of bluefish diet by weight (Table 1 and 2).

In 1992, the diet of YOY bluefish was dominated by clupeids, moronids, and bay anchovy *Anchoa mitchilli* (Table 1). Clupeids (American shad, blueback herring [*Alosa aestivalis*], alewife [*Alosa pseudoharengus*], and *Alosa* spp.—clupeids that could not be identified to species) were the dominant prey of 1992 bluefish collected by beach seine and were found in 30% of stomachs containing prey and represented 27% of bluefish prey weight (Table 1). Striped bass, white perch, *Morone americana*, and *Morone* spp. (moronids that could not be identified to species) were found in 19% of bluefish stomachs and made up 27% of their diet by weight. Bay anchovy were an important component of the diet on 19–20 Sept, representing 47% of the diet by weight (41%*F*). Atlantic silversides, *Menidia menidia*, and Atlantic tomcod, *Microgadus tomcod*, were found in bluefish diets during August and September. Invertebrates (zoeae, copepods, and sand shrimp) were a small component of bluefish diet (Table 1).

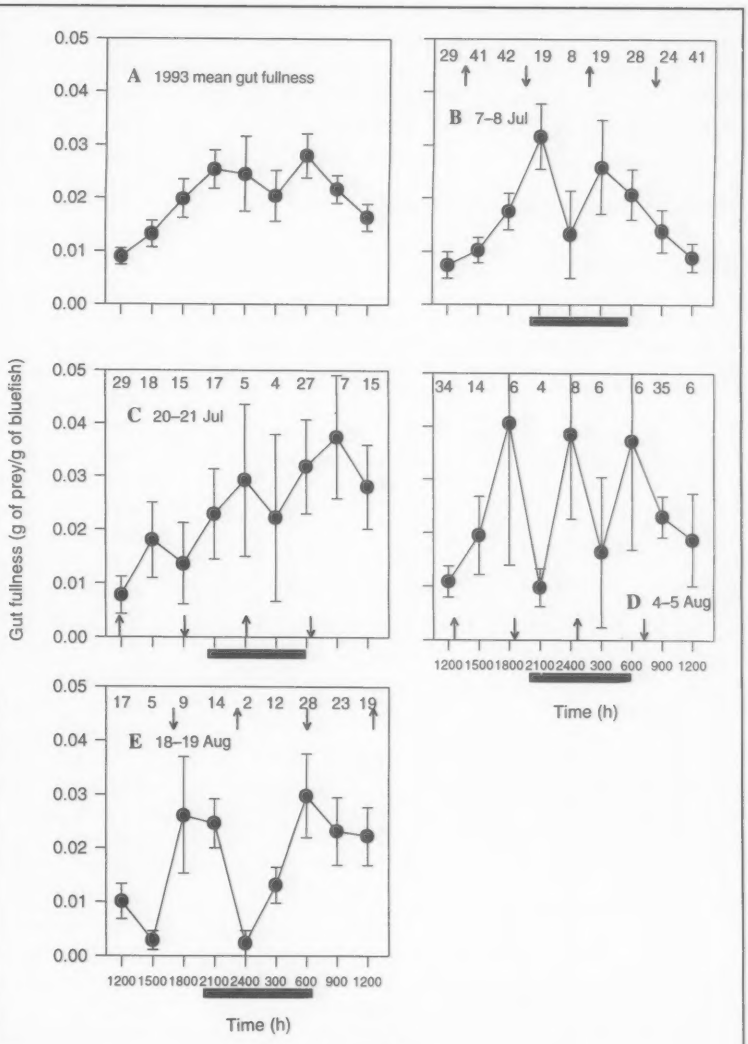
A 1993 mean gut fullness
B 7–8 Jul
C 20–21 Jul
D 4–5 Aug
E 18–19 Aug
Gut fullness (g of prey/g of bluefish)
Time (h)
1200 1500 1800 2100 2400 300 600 900 1200

Figure 4

Gut-fullness values (mean ± SE) of spring-spawned bluefish, *Pomatomus saltatrix*, versus time of capture during 1993 diel beach-seine collections. (**A**) Mean gut fullness (± SE) averaged across all dates of collection: (**B**) 7–8 July, (**C**) 20–21 July, (**D**) 4–5 August, and (**E**) 18–19 August 1993. The time periods from sunset to sunrise are indicated by dark horizontal bars. Numbers above each gut-fullness estimate represent bluefish sample size. Upward and downward facing arrows represent the time of high and low tide, respectively.

In 1993, the diet of YOY bluefish was dominated by striped bass, bay anchovy, and Atlantic silversides (Table 2). Striped bass was the dominant prey of YOY bluefish in 1993 beach-seine collections, i.e. in 22% of bluefish stomachs and accounting for 37% of their diet by weight. Bay anchovy was also a major prey of bluefish in 1993 (11%*F*, 22%*W*), particularly during the July collections. The Atlantic silverside became an important prey in August (Table 2). As in 1992, invertebrates were a small component of bluefish diet.

Striped bass (17%*F*, 35%*W*) and Atlantic silversides (24%*F*, 27%*W*) were dominant prey items of YOY bluefish captured with the gill net in 1993 (Table 3).

Clupeids and bay anchovy were also important prey items of YOY bluefish captured in the gill net. Diets of YOY bluefish captured in the surface trawl on 15–16 July 1993 were dominated by bay anchovy (56%*F*, 52%*W*) and striped bass (7%*F*, 20%*W*) (Table 3).

Discussion

Diel movements

We found large differences in the CPUE of bluefish with the diel cycle in beach-seine, gill-net, and surface trawl collections. There are several mechanisms that could account for these patterns. Rountree and Able (1993) distinguished two types of diel sampling bias: 1) direct avoidance of the gear or 2) a change in fish behavior. They further divided the second bias into diel movement between habitats (into or away from the gear sampling area) and diel changes in local activity (e.g. foraging).

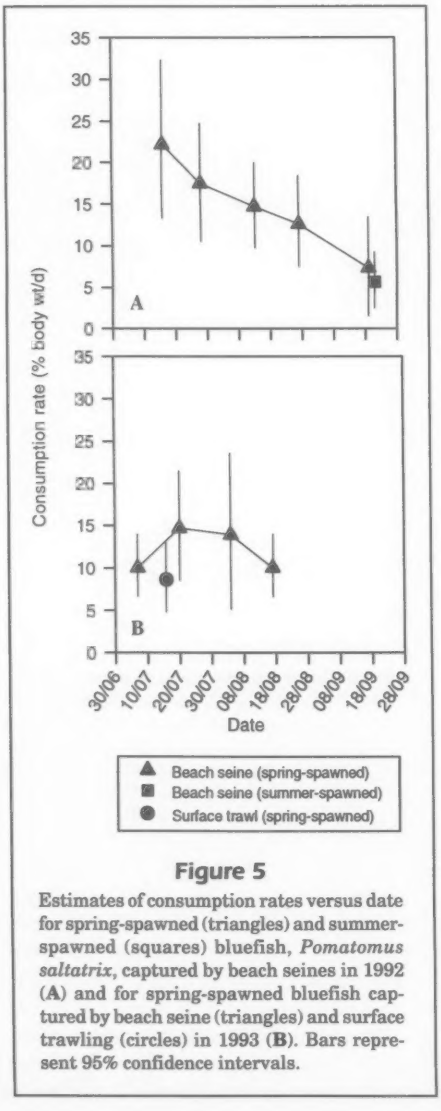

Figure 5

Estimates of consumption rates versus date for spring-spawned (triangles) and summer-spawned (squares) bluefish, *Pomatomus saltatrix*, captured by beach seines in 1992 (**A**) and for spring-spawned bluefish captured by beach seine (triangles) and surface trawling (circles) in 1993 (**B**). Bars represent 95% confidence intervals.

Catch-per-unit-of-effort of YOY bluefish (both spring- and summer-spawned cohorts) was higher during day beach-seine collections than during night collections in both 1992 and 1993 (Fig. 2, A–B). Fish would more likely detect and avoid beach-seine gear during the day than at night. Additionally, we used a boat to set the seine, which helped to standardize set time so that there were probably limited avoidance biases between diurnal and nocturnal collections due to "operator" efficiency. We therefore rule out direct avoidance of the gear (bias one) and accept a diel behavioral change (bias two) as an explanation for low night CPUE.

The surface trawl CPUE in 1993 was also highest during daylight hours (Fig. 2D). Because the pattern of CPUE in 1993 was not that expected if fish were visually avoiding the gear (bias one), we propose that a behavioral change that increases the susceptibility of bluefish to the surface trawl gear during the day is most likely responsible for the pattern.

Bluefish CPUE with the gill net was highest at sunset and night sets in 1993 (Fig. 2C). The pattern of gill-net CPUE was the opposite of what we saw with the 1993 beach-seine and surface trawl CPUE data. During the gill-net and beach-seine "movement collection" on 11–12 August 1993, beach-seine catches were higher an hour before sunset than an hour after (Fig. 2E). The opposite pattern was seen at sunrise. On this date, gill-net catches were low during the day and increased to a midnight peak before declining to zero after sunrise (Fig. 2E). We attempted to determine the direction of bluefish movement from the orientation of individual bluefish in the gill net; however, data were inconclusive.

According to beach-seine, surface trawl, and gill-net collections, bluefish occupy nearshore and surface waters during the day and then move offshore and below surface waters at night. Although we cannot rule out avoidance of gill-net gear (bias one) as a possible explanation of low day gill-net CPUE's, concomitant declines in beach-seine CPUE of bluefish in nearshore areas suggest that increased gill-net catches are at least partly a result of bluefish moving offshore. Support for our findings comes from field collections in other estuaries. Pristas and Trent (1977) found significantly higher catches of adult bluefish at night with monofilament and multifilament gill nets in shallow-water (0.7–1.1 m), mid-

Table 1

Stomach contents of spring- and summer-spawned bluefish, *Pomatomus saltatrix*, captured during diel beach-seine collections in the Hudson River estuary in 1992. *%F* = frequency of occurence, *%W* = percent wet weight.

Prey type		Spring-spawned										Summer-spawned		Spring-spawned	
		16–17 July		28–29 July		13–14 Aug.		26–27 Aug.		19–20 Sept.		19–20 Sept.		Total	
Species	Common name	%F	%W	%F	%W	%F	%W	%F	%W	%F	%W	%F	%W	%F	%W
Anchoa mitchilli	bay anchovy	13.5	11.0	5.1	1.9	3.0	0.7	10.3	1.1	41.4	47.1	19.2	18.5	15.0	18.4
Morone saxatilis	striped bass	17.5	24.4	5.1	3.9	15.2	23.7	11.8	39.0	4.6	9.5			11.8	19.6
Morone americana	white perch	2.4	1.8	6.8	5.6	6.1	10.6	1.5	1.7	1.2	2.6			3.4	4.8
Morone spp.		5.6	2.3	3.4	1.5	5.1	4.3	2.9	1.9	1.2	1.0			3.9	2.2
Alosa sapidissima	American shad	6.4	15.6	15.3	24.1	5.1	7.3	7.4	6.6	9.2	9.7	2.1	9.3	8.0	10.5
Alosa aestivalis	blueback herring	3.2	4.9	15.3	12.7	1.0	1.4							3.2	2.1
Alosa pseudoharengus	alewife			3.4	7.1	1.0	3.0							0.7	1.5
Alosa spp.		21.4	22.9	25.4	26.1	18.2	17.4	17.7	8.7	10.3	5.4	14.9	26.4	18.5	13.0
Menidia menidia	Atlantic silverside	2.3	2.3			7.1	8.6	13.2	13.8	2.3	5.2	2.1	7.7	4.8	6.9
Microgadus tomcod	Atlantic tomcod	0.8	0.4			1.0	2.2	2.9	13.4	2.3	2.5			1.4	4.0
Other fish[1]						1.0	0.1	1.5	3.0					0.4	0.5
Unidentified fish remains		38.9	12.9	52.5	16.9	49.5	20.5	41.2	10.8	39.1	14.2	55.3	33.6	43.5	15.3
Total fish			98.5		99.8		99.8		99.5		97.2		95.5		98.8
Crangon spp.	sand shrimp							1.5	0.2	4.6	1.0	8.5	4.0	1.1	0.2
Zoeae and copepods		0.8	0.5	1.7	<0.1	2.0	<0.1	2.9	0.3	1.2	1.3			3.6	0.7
Other[2]				3.4	0.2	9.1	0.2	1.5	<0.1	8.0	0.5	14.9	0.8	4.9	0.3
Total stomachs analyzed		179		83		125		85		99		64		571	
Number containing prey		126		59		99		68		87		47		439	
Mean bluefish size (g) (SE)		4.48 (0.18)		11.30 (0.69)		25.04 (1.27)		41.16 (2.78)		43.71 (2.01)		10.29 (1.29)			

[1] "Other fish" include Atlantic menhaden, *Brevoortia tyrannus*, and bluefish, *Pomatomus saltatrix*.
[2] "Other" includes vegetation, gravel, sand, and rope fibers.

water (2.2–2.6 m), and deep-water (5.2–5.6 m) zones of a Florida estuary. Using a subtidal weir in a polyhaline marsh creek in New Jersey, Rountree and Able (1993) captured a significantly higher number of YOY bluefish during day sampling than during night sampling. They concluded that this CPUE pattern was a result of diurnal foraging or increased activity (or both). Juanes and Conover (1994) made two diel beach-seine collections in Great South Bay, NY. Although they made no comparison between night and day abundance, their mean diurnal catch was two to three times higher than their mean nocturnal catch. These field studies confirm that bluefish activity patterns are influenced by light and dark cycles and that this pattern exists in diverse environments beyond the Hudson River estuary.

Factors that may be responsible for changes in diel activity or movements of fishes include foraging (Sciarrotta and Nelson, 1977; Wurtsbaugh and Li, 1985), reduction in predation risk (Clark and Levy, 1988; see Hobson, 1991), spawning (Conover and Kynard, 1984), and thermoregulation (Caulton, 1978; Rountree and Able 1993; Neverman and Wurtsbaugh, 1994). These factors may be interdependent. For example, Neverman and Wurtsbaugh (1994) found that Bear Lake (Utah-Idaho) YOY sculpin were able to digest their gut contents in a short period (overnight) by moving into warm surface waters at night. By digesting their food overnight, these fish were able to feed the following day. Clark and Levy (1988) showed that the vertical migration of juvenile sockeye salmon in an Alaskan lake during the day could be explained as a tradeoff between foraging and predation risk. For juvenile estuarine fishes, Miller and Dunn (1980) considered foraging as the primary cause of diel movements.

If bluefish movements are directly related to foraging, we might expect a strong correlation between the abundance of bluefish and their prey. Bluefish may congregate where prey density is high, or prey

Table 2

Stomach contents of spring-spawned bluefish, *Pomatomus saltatrix*, captured during diel beach-seine collections in the Hudson River estuary in 1993. *%F* = frequency of occurence, *%W* = percent wet weight.

Prey type		Date													
		7–8 July		20–21 July		4–5 Aug		11–12 Aug[1]		18–19 Aug		11–12 Sept[1]		Total	
Species	Common name	*%F*	*%W*	*%F*	*%W*	*%F*	*%W*	*%F*	*%W*	*%F*	*%W*	*%F*	*%W*	*%F*	*%W*
Anchoa mitchilli	bay anchovy	27.9	13.5	30.2	27.3	15.1	8.9	15.4	5.9	12.2	7.8	12.5	3.2	21.7	9.9
Morone saxatilis	striped bass	32.0	67.8	17.4	41.2	16.3	37.0	7.7	13.8	13.0	28.9	12.5	23.9	20.7	32.2
Alosa sapidissima	American shad					2.3	8.5			1.0	1.4			0.6	2.4
Alosa spp.				2.3	5.8	5.8	5.0	2.6	0.5	4.1	4.0			2.5	3.3
Menidia menidia	Atlantic silverside	1.2	1.2	1.2	2.5	16.3	23.1	41.0	69.7	22.5	35.9	12.5	21.0	11.5	32.8
Other fish[2]						3.5	1.7			4.1	9.0	12.5	13.2	3.4	4.3
Unidentified fish remains		40.1	14.8	48.8	21.8	40.7	10.8	25.6	7.5	45.0	12.0	75.0	37.1	42.1	13.2
Total Fish			97.3		98.6		95.0		97.4		99.0		98.4		98.0
Crangon and *Palaemonetes* spp.	sand and grass shrimp					14.0	4.6	10.3	2.6	3.1	0.3	12.5	1.6	4.1	1.6
Zoeae and copepods		6.4	2.4	1.2	0.2					2.0	0.4				
Other[3]		5.2	0.3	11.0	1.2	7.0	0.4			10.2	0.3			7.0	0.4
Total stomachs analyzed		248		137		119		47		129		23		703	
Number containing prey		172		86		86		39		98		8		489	
Mean bluefish size (g) (SE)		4.96 (0.10)		8.96 (0.51)		19.84 (0.94)		23.29 (1.41)		33.41 (1.59)		75.67 (8.79)			

[1] Bluefish that were captured on 11–12 Aug and 11–12 September were not used to calculate daily ration.
[2] "Other fish" includes killifish, *Fundulus* spp., American eel, *Anguilla rostrata*, white perch, *Morone americana*, *Morone* spp., Atlantic menhaden, and unidentifiable sciaenids.
[3] "Other" includes vegetation, gravel, sand, and rope fibers.

may leave an area of high bluefish densities. However, we found no evidence of a correlation between prey and predator abundance; although positive relations between bluefish and prey abundance were found on three out of four dates in 1993, these correlations were nonsignificant.

Sea-surface illumination was the only environmental factor describing a significant amount of the variation in nearshore CPUE of YOY bluefish. Young-of-the-year fish of several shallow-water marine fishes move inshore at night (Keats, 1990; Burrows et al., 1994). We, however, observed an opposite pattern for bluefish in our study. Given that bluefish are visual predators, diurnal schooling and foraging in the nearshore zone is a possible explanation for relatively high and variable daytime beach-seine CPUE. Olla and Studholme (1972) found that adult bluefish in the laboratory had higher activity (swimming speed) and a larger schooling group size during the day than at night. The difference in diel activity was also seen in YOY bluefish and shown to be endogenous (Olla and Studholme, 1978). Olla and Marchioni (1968) found that photomechanical changes in the retina of YOY bluefish were also internally controlled and thus lessened the time required for light and dark adaptation. Such diurnal rhythms would offer a selective advantage for a predator dependent on vision for prey capture.

Feeding period

During 1992 and 1993, gut-fullness values from bluefish caught in beach seines were highest during day, evening, and morning collections. However, there were dates in 1993 when bluefish gut-fullness levels indicated nocturnal feeding; these dates occurred with a recent full moon (7–8 July, 4–5 August) and a new moon (20–21 July). Therefore, moonlight is not entirely responsible for the nocturnal feeding seen in 1993. In laboratory tanks, YOY bluefish are capable of feeding in complete darkness (Juanes and Conover, 1994). Tide may also influence the timing of feeding; however, the timing of low and high tide had no consistent influence on peaks in gut-fullness levels (Fig. 3–4).

Table 3

Stomach contents of spring-spawned bluefish captured during surface trawl and gill-net collections in the Hudson River estuary in 1993. *%F* = frequency of occurence, *%W* = percent wet weight.

Prey type		Date							
		Surface trawl		Gill net					
		15–16 July		20 July–4 Aug		11–12 Aug		18–19 Aug	
Species	Common name	%F	%W	%F	%W	%F	%W	%F	%W
Anchoa mitchilli	bay anchovy	56.3	51.7	3.0	5.9	6.3	10.1	2.6	0.6
Morone saxatilis	striped bass	7.0	20.4	18.2	47.6	25.0	33.9	18.4	33.3
Morone spp.				6.1	5.1				
Alosa sapidissima	American shad			3.0	5.1	12.5	19.8		
Alosa aestivalis	blueback herring							2.6	3.5
Alosa pseudoharengus	alewife					6.3	8.7		
Alosa spp.		1.4	2.5	15.2	8.5			5.3	2.8
Menidia menidia	Atlantic silverside			6.1	2.9	18.8	9.0	31.6	39.1
Other fish[1]		1.4	10.2	3.0	8.7	6.3	15.2	2.6	1.2
Unidentified fish remains		43.7	13.9	51.5	15.3	25.0	1.4	44.7	19.2
Total fish			98.7		99.2		97.9		99.7
Crangon spp.	sand shrimp			3.0	0.8	12.5	2.1	2.6	0.3
Zoeae and copepods		4.2	0.5						
Total stomachs analyzed		94		83		29		71	
Number containing prey		71		33		16		38	
Mean bluefish size (g) (SE)		6.83 (0.65)		50.93 (1.81)		55.25 (3.68)		52.95 (2.44)	

[1] "Other fish" are bluefish, Atlantic menhaden, unidentified sciaenid, and American eel.

Declining gut-fullness values probably represent periods when fish do not feed. In 1992, these periods occurred mostly after sunset during nocturnal hours for both spring- and summer-spawned bluefish (Fig. 3, B–F). In 1993, declining gut-fullness values were more variable and followed sunset or sunrise peaks in gut fullness, or else not at all (Fig. 4, B–E). Bluefish that Juanes and Conover (1994) captured during diel sampling showed peaks in gut-fullness values during crepuscular periods and a subsequent decline in gut-fullness values and a higher percentage of empty guts at night.

Many freshwater, estuarine, and marine fish species show periodicity in their daily feeding (Helfman, 1979; Miller and Dunn, 1980; Reis and Dean, 1981; Popova and Sierra, 1985; Wurtsbaugh and Li, 1985; Nico, 1990; Jansen and Mackay, 1992). This periodicity is exhibited in fish that feed either diurnally, nocturnally, or during crepuscular periods. Young-of-the-year bluefish appear to be mainly diurnal and crepuscular foragers but are also able to feed at night.

Daily ration estimates

Daily ration estimates from this study are consistent with prior laboratory and field studies in which YOY bluefish were shown to have relatively high consumption rates for a temperate fish (Juanes and Conover, 1994; Buckel et al., 1995). Field estimates of bluefish consumption rates in the Hudson River estuary in early 1992 approached 25% body wt/d. In 1992, daily rations declined as fish grew. Largest values for consumption-rate rations occurred in mid-July (22.2%) and dropped to a low in mid-September (7.3%) (Fig. 5A). The pattern and magnitude of field estimates of consumption rate were similar to values of consumption rate from laboratory-mesocosm experiments made at the same time on similar-size fish (Buckel et al., 1995). In 1993, however, the early (10.1 %) and mid-July (8.6%) estimates of daily ration from 24-hour collections made with beach seines (7–8 July) and surface trawls (15–16 July) were lower than the mid-July beach-seine estimate in 1992 (16–17 July). The last three daily ration estimates in 1993

were similar to those estimated for similar dates in 1992 (Fig. 5, A and B). A comparison of these field consumption rate estimates with estimates from bioenergetic models (Steinberg, 1994; Hartman and Brandt, 1995b) is dealt with elsewhere (Steinberg and Conover[1]).

There are several possible explanations for the relatively low estimates of daily ration in early July 1993. First, these are point estimates of feeding rate that may not reflect average daily feeding over longer periods (see Smagula and Adleman, 1982; Trudel and Boisclair, 1993). Although Trudel and Boisclair (1993) found low day-to-day variation (7.0–16.3%) of daily ration for minnows in a field study, Smagula and Adelman (1982) found large day-to-day variation (30–40%) in daily ration estimates of piscivorous largemouth bass in the laboratory.

Alternatively, other factors known to affect fish consumption rates include temperature, fish size, prey availability, prey biomass, prey type and size composition, and risk of predation. Both temperatures and bluefish sizes were similar in 1992 and 1993 (Tables 1–4). Prey abundance was not recorded during diel collections in 1992 and thus cannot be compared, but there were differences in the types and sizes of prey consumed by bluefish in these years (Table 4). The much larger clupeid species were a dominant part of bluefish diet in 1992 but were not a dominant prey in 1993. This finding reflects riverwide relative abundance estimates from a separate beach-seine study (Buckel, 1997). In July 1992, clupeids, striped bass, and bay anchovy represented 90% of the available forage fish. Striped bass alone represented 63% of the available forage fish at this time in 1993. Moreover, striped bass and bay anchovy were larger for a given bluefish size in 1992 than in 1993. A combination of the size and type of prey available, along with the possible behavior differences between the prey (e.g. clupeids are more pelagic and less refuge oriented), may have caused the large differences in daily ration in July. We have no information on relative abundances of predators of juvenile bluefish in July 1992 and 1993 and therefore cannot discount predation risk as a potential mechanism explaining differences in daily ration in July.

[1] Steinberg, N. D., and D. O. Conover. 1997. Young-of-the-year bluefish (*Pomatomus saltatrix*) consumption in the Hudson River estuary: a bioenergetic modeling approach. Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000. Manuscr. in prep.

Diet analysis

Diets of YOY bluefish in 1992 and 1993 were dominated by fish prey, confirming past studies in the Hudson River estuary that have shown YOY bluefish to be largely piscivorous (Texas Instruments, 1976; Juanes et al., 1993). Diets of YOY bluefish were dominated by important anadromous resource species: clupeids in 1992 and striped bass in 1993. Interannual variation in diet was also observed by Friedland et al. (1988) in their study of YOY bluefish in a New Jersey marine embayment. Because YOY bluefish are believed to be opportunistic predators (Friedland et al., 1988; Juanes et al., 1993), the diet differences we observed appear to be a result of the availability of different prey types in 1992 and 1993 (see riverwide abundances above). However, our diet data may be biased because spatial coverage was limited to the Croton Point region of the Hudson River.

Table 4

Percentages of fish with empty stomachs, prey types, mean prey size, and mean values of temperature and gut fullness for diel collections in 1992 and 1993 (beach-seine and the 15–16 July 1993 surface trawl collection (ST)). Prey types are C = clupeids; SB = striped bass; BA = bay anchovy; and AS = Atlantic silversides. Prey types are listed in their order of importance in bluefish diet on each date. Mean prey sizes follow the order of prey type.

Year	Date	% with empty stomach	Prey type	Mean prey size (mm)	Mean temp (°C)	Mean gut fullness (g of prey/g of bluefish) (%)
1992	16–17 June	29.6	C, SB, BA	42.9, 32.9, 27.3	25.6	4.31
	28–29 July	28.9	C	45.7	25.3	3.40
	13–14 Aug	20.8	C, SB, AS	50.9, 56.1, 68.3	25.0	3.26
	26–27 Aug	20.0	SB, C, AS	68, 52, 45.2	26.7	2.27
	19–20 Sept	12.1	BA, C	43.2, 60.2	22.4	3.62
1993	7–8 July	30.6	SB, BA	26.3, 16.5	26.9	1.52
	15–16 July (ST)	24.5	BA	20.4	25.6	1.69
	20–21 July	37.2	SB, BA	39.4, 24.5	26.1	2.13
	4–5 Aug	27.7	SB, AS, C, BA	52.5, 47.0, 57.3, 35.7	25.9	2.08
	18–19 Aug	24.0	SB, AS, BA	68.3, 61.5, 40.4	24.8	2.10

Bluefish collected by gill net and surface trawls had diets that were similar to those of bluefish captured with beach seines (Table 1–3). This finding suggests that YOY bluefish feed nearshore and then move offshore or that prey types in offshore shoal feeding areas do not differ from prey nearshore (or both). However, bluefish captured by surface trawls in 1993 had a larger amount of bay anchovy in their diet than did bluefish captured with beach seines during the previous week. This finding may reflect increased availability of bay anchovy in offshore surface waters than in nearshore environments.

Implications

This study provides an improved understanding of the temporal and spatial patterns of bluefish feeding ecology in the Hudson River estuary. Knowledge of the temporal and spatial scales at which predators forage is required for a variety of predator-prey studies. Densities of predator and prey at scales relevant to predator foraging should be used for calculations of prey-type selectivity (O'Brien and Vinyard, 1974), in encounter rate models (see Brandt and Mason, 1994), in functional and numerical response calculations (Peterman and Gatto, 1978), and in calculations of a predator's growth or impact (Brandt and Kirsch, 1993; Petersen, 1994).

Empirical data on the diel changes in spatial overlap of fish and their prey and the timing of foraging activity is often lacking from spatially explicit models of fish feeding and growth. For example, Brandt and Kirsch (1993) used estimates of prey density from offshore nighttime collections. If the sampling design for estimating the densities of YOY bluefish and their prey in the Hudson River were constrained to only offshore or night (or both), the peaks in feeding activity that occur during day and crepuscular periods in the nearshore would be missed. Clearly, a detailed understanding of the spatiotemporal movement and feeding patterns of predators and prey are necessary to produce realistic models of feeding and growth (Mason and Patrick, 1993).

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Population biology and harvest of the coral reef surgeonfish *Acanthurus lineatus* in American Samoa

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Abstract.—The herbivorous blue-banded surgeonfish, *Acanthurus lineatus*, was a major species harvested on coral reefs in American Samoa, accounting for 39% by weight of artisanal catches in 1994. Spawning occurred year-round but peaked during the austral spring and summer (October–February). A dense pulse of recruits (0.4–0.6 recruits/m^2) settled onto the outer reef flat in March–April. Apparent survival was low during the first year but increased thereafter (80%/year). The fish were strongly site-attached on a daily basis, but an estimated 60% of the adults switched territories at least once during a 3-year period, thereby negating attempts to estimate mortality through attrition rates of marked individuals. Estimates of fish condition changed through the year, generally paralleling seasonal changes in a suite of environmental factors. The fish grew rapidly, attaining 70–80% of their total growth during their first year, followed by slow growth and long life (up to 18 years), characteristics that confounded standard growth analyses by producing age-specific growth parameters. Growth was best described by a two-phase von Bertalanffy growth curve for ages 0–3 (K=1.1) and ages 4–18 (K=0.12, L_∞=22.1 cm), with the separation based on the age at which 50% of the population reached maturity. Indicators of fishing pressure over a 9-year period were equivocal but did not point to significant overfishing.

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Coral reef fishes are harvested for food throughout the South Pacific islands (Wright, 1993; Dalzell et al.[1]). In American Samoa, well over 100 species are caught in artisanal and subsistence fisheries, but biological information about these species and their responses to exploitation is sparse. Moreover, these fish are often treated as taxonomic groupings rather than as individual species, and the information that is available often pertains to geographic areas distant from and dissimilar to isolated oceanic islands such as American Samoa.

The purposes of this study were to examine life history characteristics and harvest of one of the most abundant species caught in Samoa, the bluebanded surgeonfish, *Acanthurus lineatus*. This species is one component of a multispecies subsistence fishery that has declined in total catch in recent years for unclear reasons (Craig et al., 1993; Ponwith[2]; Saucerman[3]). Thus, we also examined whether overfishing accounted for declines in catches.

The herbivorous *A. lineatus* is broadly distributed throughout the Indo-Pacific and Indian Ocean regions and has been the subject of several studies on behavioral ecology (Robertson et al., 1979; Robertson and Polunin, 1981; Robertson, 1983 and 1985; Choat and Bellwood, 1985; Polunin and Klumpp, 1989; Choat, 1991; Craig, 1996). On the Great Barrier Reef of Australia, this species is long-lived; some fish live

[1] Dalzell, P., T. Adams, and N. Polunin. 1995. Coastal fisheries of the South Pacific. Workshop on management of South Pacific Inshore Fisheries, New Caledonia, 26 June–7 July 1995. Joint Forum Fisheries Agency—South Pacific Commission, Biol. Paper 30, 151 p.

[2] Ponwith, B. 1991. The shoreline fishery of American Samoa: a 12-year comparison. Dep. Mar. and Wildl. Res., American Samoa, Biol. Rep. Ser. 23, 51 p.

[3] Saucerman, S. 1995. The inshore fishery of American Samoa, 1991 to 1994. Dep. Mar. and Wildl. Res., American Samoa, Biol. Rep. Ser. 77, 45 p.

as long as 44 years (Choat and Axe, 1996). In Samoa, *A. lineatus* occurs in high densities on coral reefs (0.4 fish/m^2; Craig, 1996). It maintains feeding territories in shallow waters during the daytime but spends nights in deeper-water crevices where it is harvested by spear fishermen.

The fisheries

American Samoa has several small-scale fisheries for nearshore and offshore fishes and invertebrates (Craig et al., 1993). In 1994, the first year when all components of these fisheries were monitored, *A. lineatus* ranked second only to skipjack tuna (*Katsuwonus pelamis*) among all species harvested, accounting for 10% of the total catch of 295 metric tons (t) (DMWR[4]).

Acanthurus lineatus, a small fish averaging 18 cm fork length (FL) and 170 g, was caught in two interrelated coral reef fisheries: artisanal and subsistence harvests. Multispecies landings in these two fisheries were 76 and 86 t, respectively, in 1994 (Saucerman[3]). The artisanal fishery consisted of 56 nighttime spear divers, among whom 15 fished regularly (about 15 days per month) by free diving and scuba diving. At 28 t, *A. lineatus* accounted for 39% by weight of artisanal catches (Fig. 1). The subsistence fishery was more diverse: fish were captured by gill nets, throw nets, rod-and-reels, handlines, and by spear fishing; invertebrates were captured by hand picking and spearing. Many species were taken; *A. lineatus* accounted for only 1–3% of subsistence catches. In both artisanal and subsistence fisheries, use of destructive fishing practices (dynamite, poison) was infrequent.

[4] DMWR (Dep. Marine and Wildlife Resources), PO Box 3730, Pago Pago, American Samoa 96799. Unpubl. data.

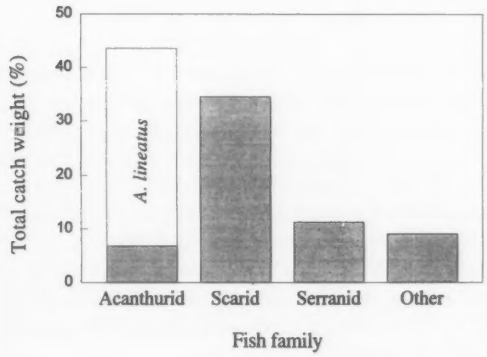

Figure 1

Catch composition (by weight) of fish families in the 1994 artisanal fishery in American Samoa. Redrawn from Saucerman (see Footnote 3 in the text).

Materials and methods

Tutuila Island in American Samoa (14°S, 171°W) is a steep volcanic island (142 km^2) with 55 km of fringing coral reef. It has two seasons, a wet summer (Oct–May) and a slightly drier and cooler season (Jun–Sep) characterized by 2.5°C cooler nearshore water temperatures and increased SE trade winds. Nearshore water temperature (taken seaward of the reef flat at 0.3 m depth) ranged from 27°C to 31°C (n=295 daily measurements). Additional details about physical variables are presented below as they relate to changes in fish condition. Rainfall and wind data were obtained from NOAA.[5]

Data were collected from 1) field studies conducted by snorkeling in shallow waters (1–4 m) on the coral reefs fronting the villages of Afao, Leone, and Matu'u (Fig. 2) and from 2) market samples of the artisanal fishery. Reef flats at the study sites were narrow (100–250 m), dropped abruptly to a depth of 3–6 m, and descended gradually thereafter to 20 m. The outer reef flat inhabited by *A. lineatus* consisted of consolidated limestone, encrusting coralline algae,

[5] NOAA (National Oceanic and Atmospheric Administration). 1994. Local climatological data, annual summary with comparative data, Pago Pago, American Samoa. National Climatic Data Center, Asheville, North Carolina, ISSN 0198-4357, 8 p.

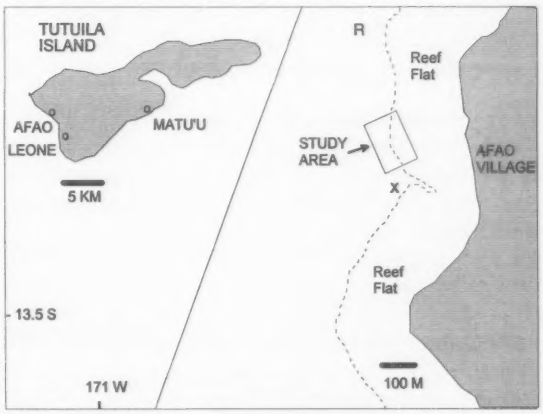

Figure 2

Tutuila Island, showing locations of study sites at the villages of Afao, Leone, and Matu'u. The main study reef at Afao (see enlargement at right) shows the spawning site of *A. lineatus* in the outer reef channel (×), the nighttime rest region (R) for *A. lineatus* using the study area, and the reef flat edge (dashed line).

and only 3.5% live coral cover (Craig, 1996). Spawning and nocturnal rest sites at Afao are shown in Figure 2 for those *A. lineatus* that maintained daytime feeding territories in the study area.

Length, weight, sex, and maturity

Length frequencies of fish in the artisanal catch were measured at 54 occasional intervals from 1987 to 1995. During 1991–94, fish were purchased at local markets to determine fork length (to the nearest mm), weight (to 0.1 g), sex, and maturity. Pooled monthly samples for these years consisted of 18–33 mature females, 18–49 mature males, and 9–116 immature fish, for a total of 1,139 fish. Maturity was assessed by visual inspection of gonads and by gonadosomatic index (GSI = $10^2 \times$ gonad weight/whole body weight). To determine maturity-at-size, immature fish whose sex could not be determined (13% of total sample) were assigned in equal proportions to numbers of identified males and females because the sex ratio of identified males and females was equal. Limited samples of rotenone-treated fish were collected at several nearshore sites in August 1990 to compare with sizes of fish taken in the artisanal fishery.

Spawning

Seasonal spawning patterns were determined from GSI trends and by conducting monthly visual surveys in the outer reef channel at the Afao site, 1993–94. Confirmation of spawning was determined by an upward rush of fish with the production of visible milt clouds.

Settlement of young onto reef

At each of the three study sites, newly settled fish in five 2×20 m permanent transects along the outer edge of the reef flat were censused monthly, approximately one week after the new moon. A repeated-measures multivariate analysis-of-variance (MANOVA with Pillai's trace test statistic) was used to test for significant differences in settlement time among the three sites and to accommodate autocorrelation of counts among observed times (Tabachnick and Fidell, 1989).

Condition factor (CF)

We used two measures of fish condition: 1) as $10^5 \times$ body weight/length^3, and 2) as the weight of the paired postabdominal fat bodies found in surgeonfishes (Fishelson et al., 1985). To examine seasonal changes, monthly mean CF values and fat body weights were compared with trends in five environmental factors that might affect fish growth: 1) nearshore water temperature, 2) available feeding hours, 3) calm surf conditions, 4) rainfall, and 5) daylength. Available feeding hours were calculated as the number of feeding hours per month during the fish's daily peak feeding period (1000–1800; Craig, 1996), minus losses of feeding time during the cooler season due to earlier sunsets and increased occurrence of spring low tides that prevented access to the fish's intertidal feeding territories. An index of calm surf conditions was calculated as the inverse of wind speed, because seasonally strong winds increase turbulence in the surf zone, thereby decreasing feeding opportunities for *A. lineatus* (Craig, 1996). Rainfall was used as a possible indicator of the amount of nutrient input into coastal waters that might, in turn, enhance growth of the algae that the fish eat. Similarly, daylength might affect algal production. Monthly means of these five factors were calculated for the years 1991–94 and presented as percentages of the maximum monthly value that occurred during this period, which were water temperature (29.6°C), available feeding period (225 h), wind speed (27 km/h), rainfall (72 cm), and daylength (13.0 h).

Growth

Growth data were fitted to the von Bertalanffy growth function (VBGF):

$$l_t = L_\infty [1 - e^{-K(t-t_0)}],$$

where l_t = length at age t;
L_∞ = asymptotic length;
K = growth coefficient; and
t_0 = time when length would theoretically be zero.

Two independent estimates of fish growth were made. In the first method, sagittal otoliths were used to estimate ages of 94 fish selected to span the widest size range possible (5.3–22.9 cm FL from pooled locations) with the methods described by Choat and Axe (1996), who aged the same species (by including tetracycline verification) from the Great Barrier Reef. Estimates of L_∞ and K were derived from a Ford-Walford regression of the age-length relation (Pauly, 1983). Estimates of t_0 were made with Pauly's (1979) empirical equation:

$$\log(-t_0) = -0.392 - 0.275 \log L_\infty - 1.038 \log K.$$

Additionally, one of each otolith pair was weighed to 10^{-4} g for comparison with fish age.

In the second method, individual growth rates were calculated for a subset of the naturally marked fish described in the field mortality study (see next section). The 57 fish selected were those for whom a time series of 4–20 size estimates was available for each fish. Lengths were estimated visually underwater; a comparison of visual estimates with actual sizes of the same fish when caught by spear indicated that the average error was 8.1 ± 1.5% (mean and SE throughout text, n=19, 6–20 cm FL).

The fish were initially selected from three general size classes according to their size at settlement onto the reef (2.5–5 cm) and approximate state of maturity based on dissection data (juveniles 6–14 cm, adults 15–23 cm). Sample sizes were 11 newly settled fish (monitored 1.7 ± 0.3 mo), 28 juveniles (5.2 ± 0.6 mo), and 18 adults (14.1 ± 1.0 mo). These fish were grouped into eight size classes of 2.5-cm intervals on the basis of their initial sizes. By using the mean growth rate of each size class, we calculated the time needed to grow to the next size class. These growth increments were plotted sequentially, forming a single growth curve for the population. A Gulland-Holt (1959) plot of growth increments of individual fish produced estimates of L_∞ and K.

Mortality

Total mortality (Z), which equals natural mortality (M) plus mortality caused by fishing (F), was estimated by monitoring the gradual loss of 145 marked fish for three years at the Afao site and by analyzing the length and age composition of fish taken in the artisanal fishery.

Field mortality Earlier work had shown that *A. lineatus* was highly site-attached (Craig, 1996); thus we initially assumed that a fish had died if it failed to re-occupy its territory or nearby area. Individual adults (n=45) and juveniles (n=50) were recognized by distinctive line patterns behind the eye and on the cheek. Sexual dimorphism was not apparent, thus males and females were not distinguished in the field. Newly settled fish (n=50) were identified by a combination of their specific location, size, color phase,[6] and line pattern when discernible. Because newly settled fish were selected on the basis of identifiability rather than first appearance in the study area, the time elapsed since settlement was not known. However, surveys were conducted frequently; therefore most newly settled fish had probably arrived within the previous week or two.

On average, about 35 fish were monitored at any one time; new individuals were added when others either outgrew their size class or were not relocated after three successive surveys. Small fish were inspected at least twice each week, larger fish about once per week. All three size groups were intermixed on the outer reef flat.

To calculate mortality, all fish within a size group were aligned to a common starting date. For each size class, mortality at any given time equalled 1 – (no. fish alive + no. fish outgrowing size class)/(initial no. fish in that size class). This approach 1) underestimated mortality for newly settled fish if there had been high mortality during the first days of settlement before observations began, or 2) overestimated mortality if observed fish emigrated from the study area. Total mortality (Z) was calculated as the slope of the descending limb of the "catch curve" (a plot of the natural logarithm of fish remaining each year versus relative age). Annual mortality was estimated as $1 - e^{-Z}$ (Ricker, 1975).

Total mortality Total mortality for harvested fish was estimated in several ways: 1) length-converted catch curves (Pauly, 1983); 2) the relation between Z and mean length of fish in the catch:

$$Z = K(L_\infty - L_c)/(L_c - L'),$$

where L_c = the average length of fish greater than length L'; and
L' = the size at which fish are assumed to be fully recruited to the fishery (Beverton and Holt, 1957);

and 3) Hoenig's (1983) empirical relation between Z and a population's longevity:

$$\ln(Z) = 1.46 - 1.01 \ln(t_{max}),$$

where t_{max} = maximum age.

Natural mortality Natural mortality (M) was estimated with two empirical equations:

$$\log M = 0.007 - 0.279 \log L_\infty + 0.654 \log K + 0.463 \log T \text{ (Pauly, 1980)}, \quad (1)$$

where T = the average monthly water temperature in the study area (28.6°C), and

$$\ln(M/K) = 0.30 \ln(T) - 0.22 \text{ (Longhurst and Pauly, 1987)}. \quad (2)$$

[6] Color phases of newly settled *A. lineatus* are not described in the literature. The "light" phase is that of adult coloration; the "dark" phase is light-to-dark gray (overlying a faint adult color pattern) and the caudal fin is orange (differentiated from dark newly settled *Ctenochaetus striatus* which have orange only on caudal fin tips).

Biological characteristics of harvest

Length-based estimates of maturity and age were calculated for artisanal catches. Additionally, in 1994–95 we measured the catches of 19 groups of 1–4 fishermen (n=43) who had fished together, to determine their average catch per unit of effort (CPUE: kg/h per person). The principal method was spear fishing by free diving; data are presented for that gear only.

Results

Length, weight, sex, and maturity

A complete size range of newly settled, juvenile and adult *A. lineatus* was present in rotenone-treated samples from shallow nearshore waters <2 m deep (Fig. 3), but large fish were underrepresented because some avoided capture. Night spear fishermen harvested the larger fish, generally 15–21 cm FL.

Males and females taken in the fishery were of similar length (t=0.26, df=993, P=0.8) and the sex ratio was nearly equal (1 male:1.1 females, n=995). Length-weight relations for the sexes did not differ significantly (ANOVA, F=0.07, P=0.79); thus all fish were pooled, including smaller unsexed fish: log weight (g) = −1.60 + 3.03 log length (FL in cm)(r^2=0.99, n=1,047). The relation between FL and standard length in cm was SL=0.86(FL) − 0.38 (r^2=0.99, n=94).

Mature fish of both sexes generally had well-developed gonads (6.2 ± 0.2 g, n=529) or gonads that appeared to be partly or wholly spawned out (1.2 ± 0.1 g, n=108). Immature fish had little gonad development (0.2 ± 0.01 g, n=502). Fish reached sexual maturity at 15–21 cm FL (Fig. 4), with males maturing at a slightly smaller size than females. Half of both sexes were mature at about 18 cm, i.e. at approximately 4 years of age.

Spawning

The gonadosomatic index (GSI) was highest during October–February (Fig. 5) and was strongly correlated with daylength and feeding hours (Table 1). Spawning also occurred throughout the year. During all months, groups of 50–200 fish were observed spawning at dawn in the outer portion of the outer reef channel at Afao (see Fig. 2). Additional details are provided elsewhere (Craig, in press).

Settlement of young onto reef

Newly settled fish (n=575) exhibited both light (79%) and dark (21%) color phases.[6] Settlement peaked in March–April with densities of 0.4–0.6 recruits/m^2 on

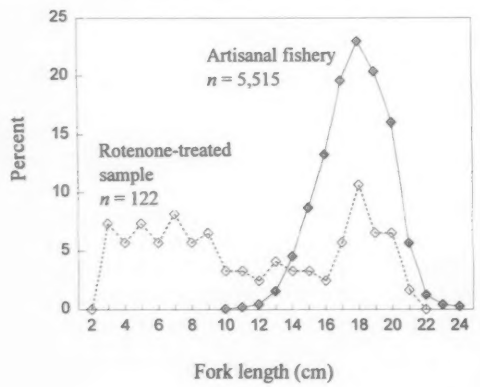

Figure 3

Sizes of *A. lineatus* in the artisanal fishery, all years combined (1987–95), and those collected in rotenone-treated shallow waters.

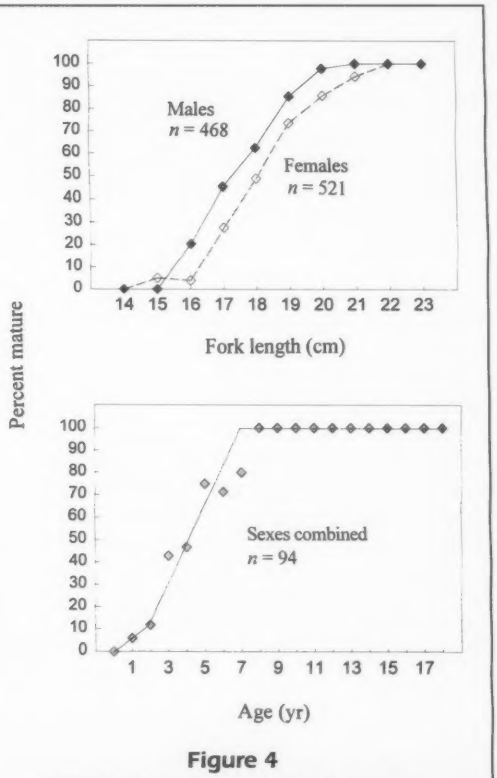

Figure 4

Length and age at maturity for *A. lineatus*.

the outer reef flat (Fig. 6). The settlement pulse occurred one month earlier at Matu'u as indicated by the significant site-time interaction detected by the repeated-measures MANOVA (P=0.03, F=4.67, numerator df=22, denominator df=6). In previous years, similar large pulses occurred in earlier months (Nov–Mar; senior author, pers. obs.).

Seasonal changes in fish condition

Fish condition factor (CF) peaked in summer and declined rapidly thereafter (Fig. 7). For mature fish, a decline in CF after the spawning season was expected, but a similar decline was evident among immature fish. Postabdominal fat bodies also declined

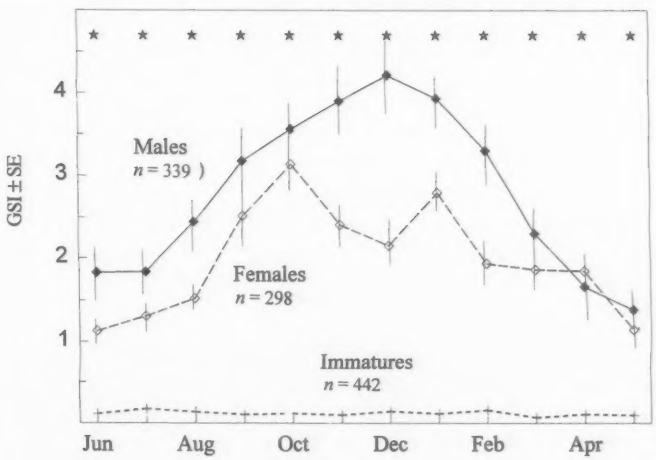

Figure 5

Monthly gonadosomatic index (GSI) for mature males and females, and immature *A. lineatus*, 1991–94 combined. Also shown are months when spawning was directly observed at Afao (stars).

Table 1

Correlation coefficients between monthly averages for physical and biological variables: gonadosomatic index (GSI), condition factor (CF), and paired fat bodies of *A. lineatus*. P = probability value.

	Water temperature	Daylength	Calm surf index	Rainfall	Feeding hours
GSI: mature fish	0.034 P>0.1	0.906 P<0.001	0.418 P>0.1	0.36 P>0.1	0.817 P<0.01
GSI: immature fish	0.347 P>0.1	0.129 P>0.1	0.252 P>0.1	0.335 P>0.1	0.311 P>0.1
CF: mature fish	0.495 P>0.1	0.703 P<0.02	0.65 P<0.05	0.667 P<0.02	0.511 P<0.1
CF: immature fish	0.846 P<0.001	0.546 P<0.1	0.925 P<0.001	0.706 P<0.02	0.343 P>0.1
Fat bodies: mature fish	0.77 P<0.01	0.228 P>0.1	0.702 P<0.02	0.491 P>0.1	0.036 P>0.1

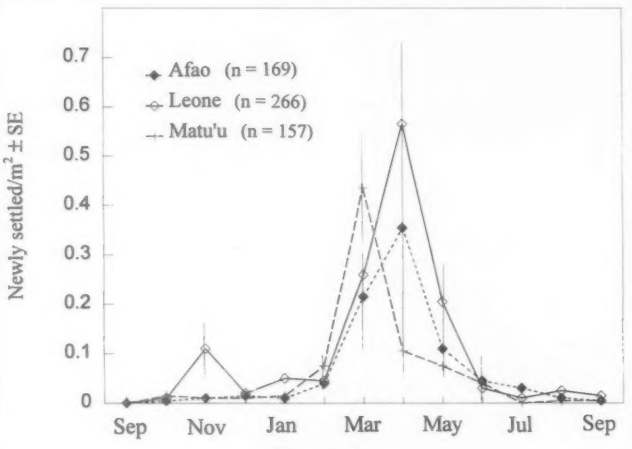

Figure 6

Monthly counts of newly settled *A. lineatus* on the outer reef flat at three sites on Tutuila Island, 1994–95.

steadily from early summer through the cooler season (Fig. 8). These losses resulted in CF values that were about 10% below peak summer levels and in fat bodies that were about two thirds below peak levels.

Seasonal changes in five environmental factors paralleled changes in fish condition (Fig. 8). During the cooler season, nearshore water temperatures dropped below maximum summer values (–9%), as did available feeding hours (–14%), calm water conditions (–44%), rainfall (–76%), and daylength (–13%). Most physical factors were significantly autocorrelated (7 out of 10 comparisons), indicating that there is a distinctive seasonal signal in the nearshore environment, despite Samoa's open-ocean location near the equator. Monthly CF values for immature and mature fish were significantly correlated with 3 of the 5 physical factors (Table 1). It seems clear that the fish were responding to a seasonal change, but causative factors are not known.

Growth

Otolith-based ages and size determinations of naturally marked fish provided two estimates of *A. lineatus* growth. Otolith weight was highly correlated with the number of annular bands in an otolith (Fig. 9). The fish grew rapidly, attaining 70–80% of their total growth by the end of their first year, and they were long-lived—up to 18 years (Fig. 10). Field estimates of fish growth confirmed the rapid early growth but underestimated later growth in comparison with the otolith-based determinations. Similar values of K and L_∞ were derived from both the otolith-based age-length relation (Ford-Walford regression: K=0.7, L_∞=20.3 cm, r^2=0.93) and from size increments of marked fish (Gulland-Holt plot: K=0.8, L_∞=21.0 cm, r^2=0.58).

However, L_∞ and K were highly dependent on the age range of fishes examined (Fig. 11). Iterative Ford-Walford regressions of the smoothed mean size at age showed that K dropped progressively from 0.8 for the whole sample (ages 0–12) to 0.1 when juvenile fish ages 0–3 were excluded. Asymptotic length (L_∞) increased in a similarly systematic manner from about 20 cm to 22 cm. Therefore, separate VBGF growth curves were generated for the juvenile phase (ages 0–3, K=1.1, t_0 =–0.2, [L_∞=18.3 cm]) and adult phase (ages 4–12, K=0.12, L_∞=22.1 cm, t_0=–15.6), a separation based on the age at which 50% of the population was mature (age 4, Fig. 4). The two-phase curve captured the precocious growth and attained a larger, more realistic L_∞ that approached the maximum size of fish taken in the fishery (see Fig. 3). Using the relation that longevity is approximated by $3/K$ (Pauly, 1983) and the adult K-value derived for ages 4–12, we predicted that the maximum age would be 25 years, which compared favorably with the observed maximum age of 18 years.

Mortality

Mortality indices differed among the three size classes of naturally marked fish at the Afao site (Fig. 12). Only 2% of the newly settled fish and 34% of the juveniles appeared to survive and grow into the next

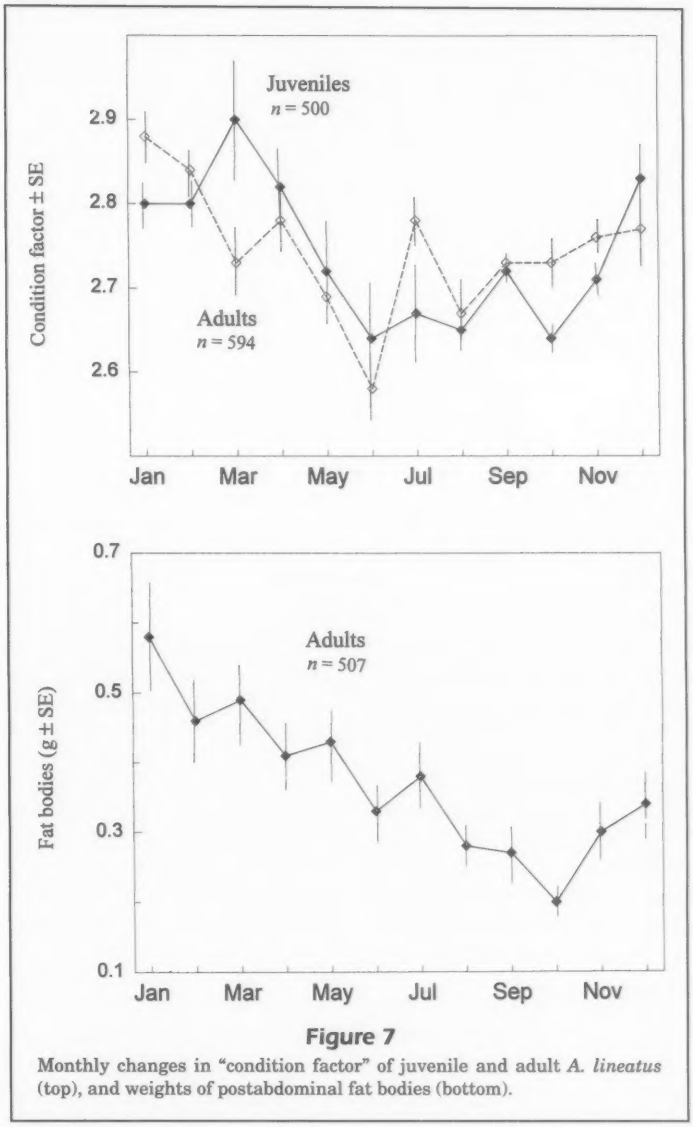

Figure 7

Monthly changes in "condition factor" of juvenile and adult *A. lineatus* (top), and weights of postabdominal fat bodies (bottom).

larger size class. At these rates, only 1% (2% × 34%) of the population would survive their first year on the reef. Thereafter numbers of marked adults declined rapidly at a loss of 48%/yr (Z=0.65). At these rates, the life span of combined life history stages would only be about 4–5 years. However, longevity, as revealed by otolith analysis, indicated that field mortality of marked fish was greatly overestimated. Mean ages of artisanal catches were 4–6 years (see below) and some fish lived up to 18 years. It is therefore likely that some marked fish emigrated from the study area rather than died (see "Discussion" section).

To obtain a more realistic estimate of adult mortality, the annual loss of fish in each age class of the 1994–95 fishery was examined by length-converted catch curves calculated in two ways: 1) after conversion with the VBGF parameters for adult fish (Pauly, 1983), and 2) after graphical conversion of lengths to ages based on the weighted length-age relation derived by otolith analysis. The latter was included because of the variability of the VBGF parameters shown in Figure 11. For fish that were assumed to be fully recruited to the fishery, total mortality was low in both cases (Z=0.24 and 0.23; Fig. 13), equat-

ing to an annual loss of about 20%. Similar values were obtained with Hoenig's equation (Z=0.23) and Beverton and Holts' relation between Z and mean length of fish in the catch (Z=0.19, K=0.12, L_∞=22.1 cm, L_c=19.6, L'=18 cm).

Natural mortality (M) was estimated to be 0.2 and 0.45 with the empirical equations of Longhurst and Pauly (1987) and Pauly (1980), respectively, and with the adult values of K and L_∞. The lower value indicated that M is equivalent to Z; the latter value was spurious given that it exceeded Z.

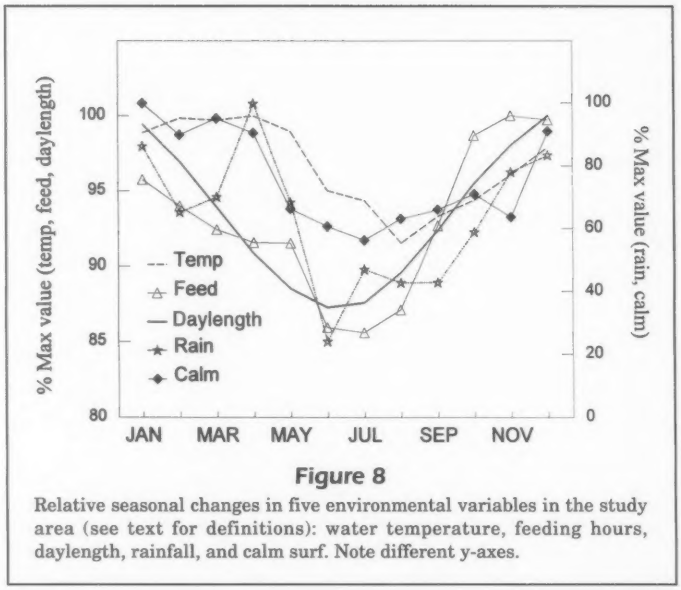

Figure 8

Relative seasonal changes in five environmental variables in the study area (see text for definitions): water temperature, feeding hours, daylength, rainfall, and calm surf. Note different y-axes.

Biological characteristics of harvest

The flattened growth curve exhibited by older *A. lineatus* limited analyses based on length-converted ages, but the conversion did indicate that most fish taken in the fishery were relatively young (Fig. 14). During the 9-year period 1987–95, annual catches varied moderately in mean age (3.6–6.2 years), mean length (17.5–19.3 cm FL), proportions of immature fish taken (29–60%), and total mortality (0.16–0.31)(Table 2). No trends in these variables were apparent, with one exception: the maximum size of fish decreased. Maximum sizes of fish in 1987–88, however, seem unrealistically high (Fig. 14), and in any case, mean sizes in later years (1994–95) were significantly larger than in earlier years (1987–88)(t=9.7, df=5088, P<0.001).

Although the more detailed 1994–95 market data spanned a relatively short period (Fig. 15), available data indicated no decrease in fish size (r=0.28, df=17, P>0.1) or CPUE over time (r=0.41, df=17, P=0.085), and no relation between fish size and CPUE at various island-wide fishing sites, i.e. sites with low CPUE did not have smaller fish (r=0.28, df=17 P>0.1).

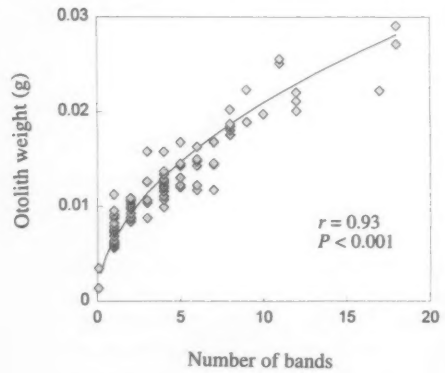

Figure 9

Relation between otolith bands and otolith weight: log (age) = 4.34 + 1.99 log (otolith wt.), n=88.

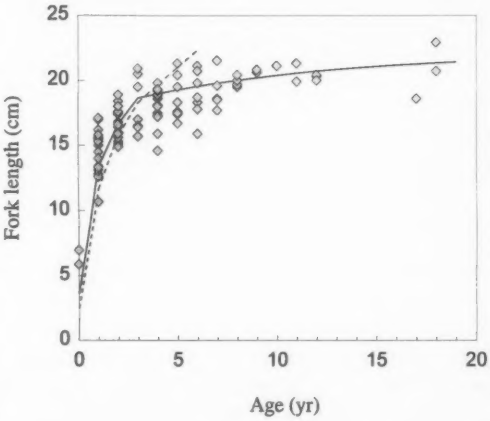

Figure 10

Age-length relations for *A. lineatus*. The solid line indicates a two-phase von Bertalanffy curve for ages 0–3 and 4–18; the dashed line indicates the growth of naturally marked fish based on visual estimates of fish size over time.

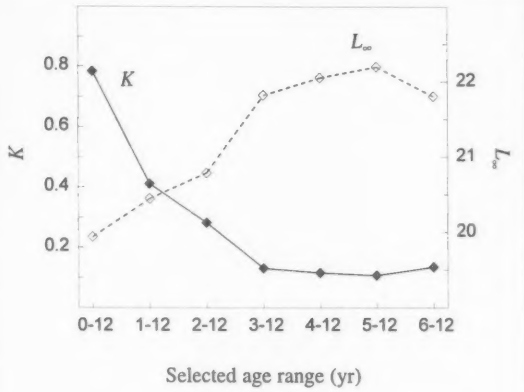

Figure 11

Changes in K and L_∞ based on iterative Ford-Walford regressions that progressively excluded age classes of younger fish. Age-length data used in this calculation were derived from a smoothed line of mean size at age.

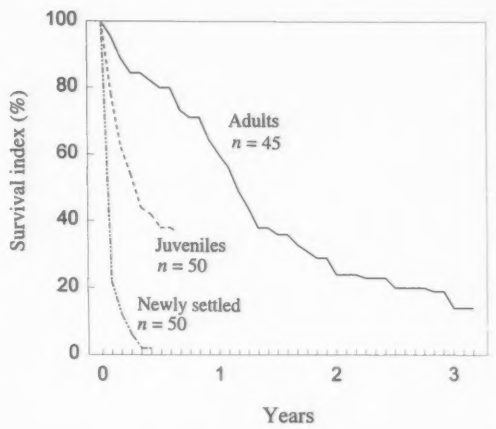

Figure 12

Survival index (percentage of fish returning to their territories) for newly settled, juvenile and adult *A. lineatus* at the Afao site.

Discussion

The life history traits exhibited by *A. lineatus* are common among coral reef fishes (e.g. Sale, 1991): it is a territorial fish that spawns year-round but primarily during the austral summer, its pelagic young settle onto the reef in a dense pulse and suffer high mortality, survivors are sedentary but occasionally relocate to new sites, and the fish grow rapidly, have relatively low mortality rates after their first year and may live for many years. Of particular interest in this study was the opportunity to examine fishing pressure on a coral reef species. In this instance, the possiblity of emigration rates of a "highly site-attached species" and the rapid initial growth pattern provide a useful context for examining the fisheries data. Additionally, because another data set is available for this species, we were able to compare locality-specific demographic traits.

Emigration

Acanthurus lineatus is strongly site-attached (adult fish have a 99.9%/day return rate to the same site: Craig, 1996), but it occasionally switches territories. After 3 years of monitoring, 6 of the 45 marked adults remained on site (Fig. 12), whereas 23 adults would have been present with an annual mortality rate of 20% as determined by catch curve. The difference (17/45) indicates that 38% of the adults that disappeared had probably emigrated to other sites. Craig

Table 2

Size, age, maturity, and mortality of *A. lineatus* in the artisanal fishery in American Samoa, 1987–95. n = sample size.

	1987	1988	1990	1994	1995
Mean FL (cm)	18.2	17.6	18.9	19.3	18.0
SE	0.04	0.1	1.0	0.5	0.7
Maximum FL (cm)	27.7	28.9	22.4	23.0	23.0
Mean length-converted age	4.6	3.6	5.7	6.2	4.1
Percent immature	46	60	37	29	53
Total mortality (Z_1)	0.22	0.23	0.19	0.23	0.25
(Z_2)	0.25	0.16	0.31	0.23	0.23
n	2,499	1,126	329	720	745

Z_1 = Z derived from a catch curve based on length-converted ages with "adult" VBGF parameters.
Z_2 = Z derived from a catch curve based on graphical conversion of length to age with the age-length relation.

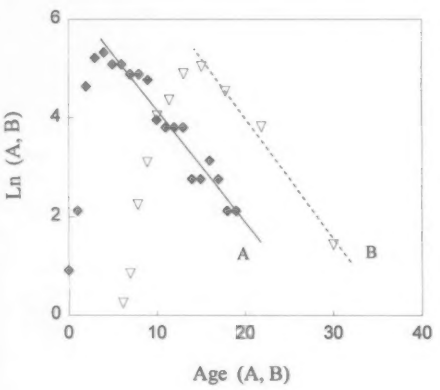

Figure 13

Catch curves for *A. lineatus* in the combined 1994–95 fishery, based on length-converted ages determined (**A**) graphically from the weighted age-length relationship, and (**B**) using VBGF parameters for adult fish (Pauly, 1983). Graph axes and Z values: (A) Ln (N) × estimated age, Z=0.23, r^2=0.98; (B) Ln (N/dt) × relative age, Z=0.24, r^2=0.95 (where N is the number of fish in a given length class and dt is the time taken to grow through that length class).

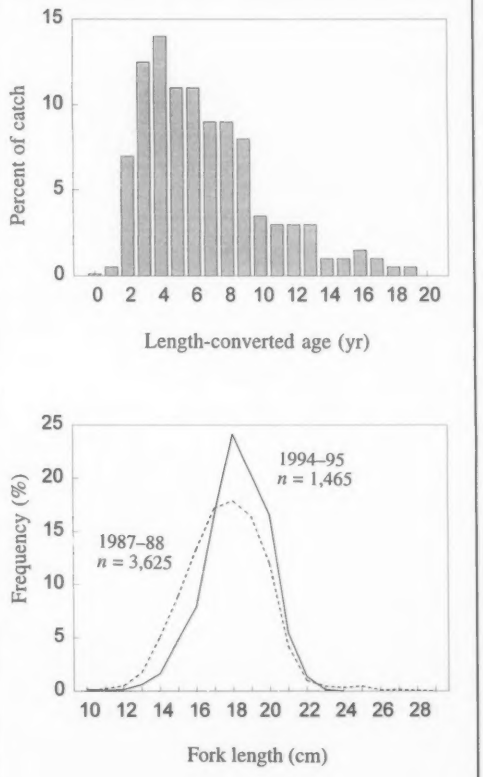

Figure 14

Length-converted age frequency of the 1994–95 fishery (top) and a comparison of length frequencies of *A. lineatus* in the 1987–88 and 1994–95 fisheries (bottom).

(1996) also monitored the same marked fish described in the present study and reported that an additional 22% of the adults changed territories to nearby locations and were relocated (for the purpose of calculating mortality, these fish were not of course considered deaths). Altogether then, about 60% of the adults changed territories at some point during the 3-year period of observation. This analysis is not thought to be complicated by the loss of fish due to fishing mortality (F), because the 20% mortality rate incorporated F. Further, Afao was a lightly fished area (senior author, unpubl. data).

Emigration probably also accounted for the loss of many juveniles and newly settled recruits shown in Figure 12. Although the annual input of recruits to the reef was high, the observed "survival" rate of these fish during their first year (1%) could not maintain the standing stock of adult fish. To illustrate, the adult density of 40 fish/100m^2 (Craig, 1996) would lose 8 fish/100m^2 per year at an annual loss of 20%. To replace those fish with newly settled fish (with an annual input rate of 100 recruits/100m^2 per year), a survival rate of 8% would be required during their first year.

Growth pattern

The rapid growth of young *A. lineatus* was so pronounced that initial VBGF analyses produced age-dependent estimates of L_∞ and K. The fish attained most of their adult size during their first year, even though the species was long-lived. There is increasing evidence that this growth pattern is common among coral reef fishes (Choat and Axe, 1996; Hart and Russ, 1996; Newman et al., 1996; Williams et al.[7]). Standard applications of growth models may be inappropriate for populations exhibiting these growth characteristics. Use of a two-phase von Bertalanffy growth curve (e.g. Soriano et al., 1992; Ross et al., 1995) is a possible solution, although care must be taken to establish consistent procedures for separating the two phases of the curve.

[7] Williams, D., S. Newman, M. Cappo, and P. Doherty. 1995. Recent advances in the ageing of coral reef fishes. Workshop on management of South Pacific Inshore Fisheries, New Caledonia, 26 June–7 July 1995. Joint Forum Fisheries Agency—South Pacific Comm., Biol. Paper 74, 5 p.

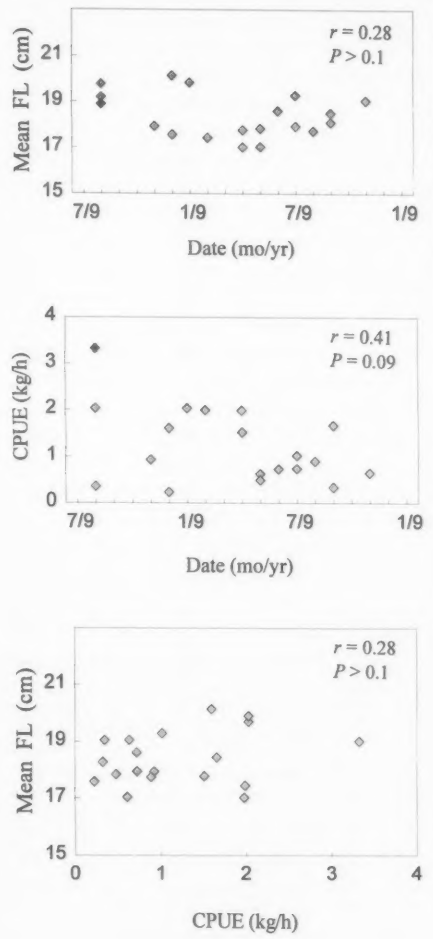

Figure 15

Size and CPUE of *A. lineatus* in the artisanal fishery from varied sites around Tutuila Island, 1994–95.

Comparison of Samoan and Great Barrier Reef (GBR) populations

There are noteworthy differences between *A. lineatus* populations off Samoa and those on the GBR. Fish grow larger and live up to twice as long on the Great Barrier Reef than those off Samoa (Fig. 16); they are also more sparsely distributed and have lower recruitment rates of newly settled young (Choat and Bellwood, 1985; Choat and Axe, 1996; Craig, 1996; Choat, unpubl. data). Reasons for these differences are speculative and may be complicated by the existence of a fishery in Samoa (see section below). Perhaps *A. lineatus* in Samoa is comparatively short-lived and maintains its abundance by a high annual input of newly settled young. Why there should be a greater abundance of newly settled fish in Samoa, an oceanic island, than in the extensive reef network of the GBR is unclear.

Fishing pressure

For at least the past 18 years, the catch composition of fish taken by night spear divers has not changed greatly, particularly with respect to the prominent catch of surgeonfishes (Fig. 17). Although Wass[8] did not identify the species composition of the 1977–80 subsistence catch, local residents report that *A. lineatus* has always been a plentiful and popular food fish.

Indicators of current levels of fishing pressure were ambiguous. Some evidence indicated that overall fishing pressure was low: 1) survival rates of fish age 1 year and older were high (80% per year), 2) estimates of total mortality and the mean size of fish in the fishery changed little over a 9-year period, 3) there was no relation between fish size and CPUE, and 4) an estimate of natural mortality was similar to that of total mortality. However, some of these points are not overly persuasive. First, estimates of natural mortality were derived from empirical equations that embody considerable variability (Gulland, 1984). Second, trends based on fish size are of uncertain value as indicators of fishing pressure due to fish behavior. At night, when *A. lineatus* is harvested, there is an apparent spatial separation of small and large fish. Fish less than about 14 cm are not often encountered in the areas fished (senior author, pers. obs.), perhaps because they remain in shallower areas or hide within smaller crevices during the night. Thus the larger sizes of fish taken by the spear fishermen represent those that were available to them, i.e. there was little opportunity for size selection. Consequently, the mean size of fish harvested could remain relatively stable under increasing levels of fishing pressure until there were no more fish left to catch.

Indications that fishing pressure was affecting the population included 1) decreases in maximum size of fish over a 9-year period, 2) the absence of very old fish in the Samoan population compared with the GBR population, as might be expected in a fished population, and 3) a possible decrease in CPUE. These points, too, are less than compelling. First, the

[8] Wass, R. 1981. The shoreline fishery of American Samoa, past and present. *In* J. Munro (ed.), Marine and coastal processes in the Pacific: ecological aspects of coastal zone management: proceedings of the UNESCO seminar at Motupore Island Research Center, 1980, p. 51–63. United Nations Education, Scientific and Cultural Organization, Paris.

decrease in maximum size was counterbalanced by a significant increase in the mean size of the catch during the same period (Fig. 14). Second, the comparison with GBR may not be valid, because natural longevities of the two populations may differ. The two populations are nearly 5,000 km apart and they dwell in different water temperature regimes; thus some geographic variation is likely. Third, the possible CPUE decline was not statistically significant and was also compromised by occasions when fishermen targeted species other than *A. lineatus*. One group of fishermen we interviewed had been told before diving that the fish buyer already had enough *A. lineatus*, thus some low CPUE values may indicate a saturated market rather than a depleted stock.

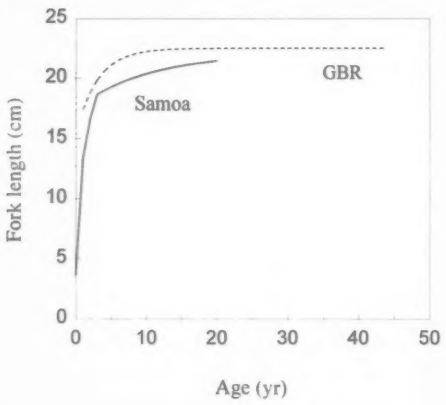

Figure 16

Growth rates of *A. lineatus* from American Samoa and the Great Barrier Reef (latter data from Choat and Axe, 1996).

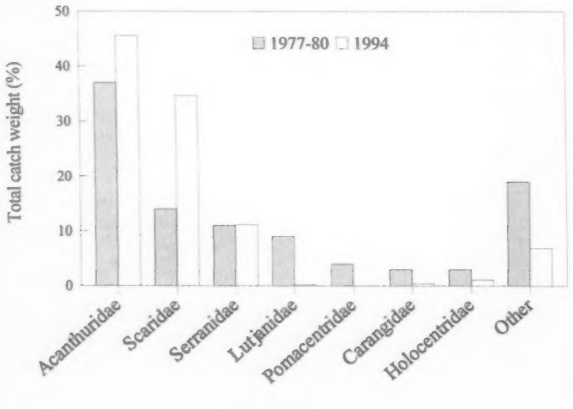

Figure 17

Comparison of catch composition (by weight) of fish families taken by subsistence night divers in 1977–80 (see Footnote 8 in the text) and artisanal night divers in 1994 (see Footnote 3 in the text).

Given the indefinite nature of these indicators, it remains unclear whether fishing pressure is having a significant effect on the demographics of *A. lineatus*, but the composite picture does not indicate substantial overfishing. We acknowledge, however, that localized overfishing is a distinct possibility. Villagers often complained that the night spear fishermen had depleted fish stocks along their village coastline. Although the artisanal fishermen generally rotated areas fished to maximize their CPUE, the villagers living near the area fished might be left with a diminished resource for a period of time.

An additional concern is that an increase in fishing efficiency was in progress in 1995, with a conversion from free diving to scuba diving. Catch-per-unit-of-effort for scuba diving was more than twice that of free diving (3.8 vs. 10.5 kg/h for all species combined). A further concern is that the human population of American Samoa, like that on many other South Pacific islands, is increasing rapidly; thus the demand on nearshore resources seems likely to increase (Craig[9]).

The lack of overt signs of fishing stress for *A. lineatus* in the artisanal fishery is at odds with observed declines in the subsistence fishery on the same coral reefs. Multispecies subsistence catches dropped from 265 and 311 t in 1979 and 1991 (Ponwith[2]; Wass[8]), to 48 t 1995 (Saucerman[3]). Catches of *A. lineatus*, a minor component in this fishery, dropped from 8 t in 1991 to 1 t in 1995. Although some of this decline may be attributed to reduced fishing effort, CPUE for most gear types declined as well (Saucerman[3]).

Causes of reduced subsistence catches are not clear but may include a variety of factors such as fishing for selected species, a reduced reliance on subsistence fishing, and habitat degradation (Craig et al.[10]). Coral reefs in American Samoa have been severely damaged in the past 15 years by three hurricanes, an *Acanthaster* starfish invasion, temperature rises that resulted in mass coral bleaching, and sedimentation from land. Whether these en-

[9] Craig, P. 1995. Are tropical nearshore fisheries manageable in view of projected population increases? Workshop on management of South Pacific Inshore Fish., New Caledonia, 26 June–7 July 1995. Joint Forum Fisheries Agency—South Pacific Comm., Biol. Paper 1, 6 p.

[10] Craig, P., A. Green, and S. Saucerman. 1995. Coral reef troubles in American Samoa. South Pacific Comm., New Caledonia, Fish. Newsletter 72:33–34.

vironmental disturbances have affected fish catches is not known, but it seems possible that these changes may have contributed to the current abundance of *A. lineatus* by creating expansive areas of denuded habitat suitable for the growth of turf algae that *A. lineatus* eats (Craig, 1996). As previously mentioned, live coral covered only 3.5% of the outer reef flat zone inhabited by this species, i.e. over 90% of the habitat seemed ideal for turf algae and *A. lineatus*. As the reefs recover, we speculate that *A. lineatus* may decrease in abundance and become less dominant in artisanal catches.

Acknowledgments

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Spatial and temporal variation in age and growth of king mackerel, *Scomberomorus cavalla*, 1977–1992

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Abstract.–A total of 12,180 king mackerel, *Scomberomorus cavalla*, collected from 1986 to 1992 from North Carolina to Yucatan, Mexico, and 2,033 collected in 1977 and 1978 from North Carolina to Texas were aged with whole or sectioned sagittal otoliths. Data were analyzed by region—Atlantic Ocean, eastern Gulf of Mexico, and western Gulf—reflecting the currently recognized stocks. Maximum sizes of females aged were 152, 158, and 147 cm FL in the Atlantic, eastern Gulf, and western Gulf, whereas the largest males were 121, 127, and 117 cm FL in those same regions. Maximum ages from the 1986–92 fish were 26, 21, and 24 yr for females and 24, 22, and 23 yr for males in the Atlantic, eastern Gulf, and western Gulf, respectively. Females grew faster and larger than males at every age in each region. A very consistent pattern of greatest growth in the eastern Gulf, intermediate in the western Gulf, and least in the Atlantic was present each year during 1986–92, most noticeably among females. During 1977–78, Atlantic females also had distinctly lower growth than Gulf fish. These consistent regional differences support the current hypothesis that there are three stocks as suggested by previous analyses of other types of data. Within a region and sex, growth was lower in 1977–78 than in 1986–92 in both the Atlantic and eastern Gulf, but higher for western Gulf females.

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Fishery Bulletin 95:694–708 (1997).

King mackerel, *Scomberomorus cavalla*, are economically valuable and highly sought after by U.S. recreational and commercial fishermen from North Carolina to Texas (Manooch, 1979). They also support a substantial commercial fishery in Mexico (Gulf of Mexico and South Atlantic Fishery Management Councils[1]) Some populations have been overfished and since 1983 the species has been managed by a joint fishery management plan of the Gulf of Mexico and South Atlantic Fishery Management Councils.[2] The species is managed as two stocks, an Atlantic migratory group and a Gulf migratory group, although the Councils recognize that there are actually two groups in the Gulf—an east and a west (Grimes et al., 1987; Johnson et al., 1994; Gulf of Mexico and South Atlantic Fishery Management Councils[3]). However, the paucity of data from the large Mexican fishery, which has a major impact on the western Gulf stock, precludes managing the two Gulf groups separately. Because tag return data (Sutter et al., 1991) collected during 1975–78 indicated considerable seasonal movement between the Gulf of Mexico and Atlantic Ocean, the boundary between the Gulf and Atlantic stocks was defined as the Volusia-Flagler County line off northeast Florida during November–March and the Monroe-Collier County line off southwest Florida during April–October. The Gulf stock has been heavily overfished throughout much of its management history, unlike the Atlantic stock, which has never been considered overfished (Mackerel Stock Assessment Panel[4]).

[1] Gulf of Mexico and South Atlantic Fishery Management Councils. 1992. Amendment 6 to the fishery management plan for coastal migratory pelagics in the Gulf of Mexico and South Atlantic. Gulf of Mexico Fishery Management Council, The Commons at Rivergate, 3018 U.S. Highway 301 North, Suite 1000, Tampa, FL 33619-2266; and South Atlantic Fishery Management Council, Southpark Building, Suite 306, 1 Southpark Circle, Charleston, SC 29407-4699, 35 p.

[2] Gulf of Mexico and South Atlantic Fishery Management Councils. 1982. Fishery management plan, final environmental impact statement, regulatory impact review, final regulations for coastal migratory pelagic resources (mackerels) in the Gulf of Mexico and South Atlantic region. Gulf of Mexico Fishery Management Council, Tampa, FL; and South Atlantic Fishery Management Council, Charleston, SC, var. pagination.

[3] Gulf of Mexico and South Atlantic Fishery Management Councils. 1990. Amendment Number 5 to the fishery management plan for the coastal migratory pelagic resources (mackerels), 33 p. Gulf of Mexico Fishery Management Council, Tampa, FL; and South Atlantic Fishery Management Council, Charleston, SC, 33 p.

[4] Mackerel Stock Assessment Panel. 1994. 1994 report of the mackerel stock assessment panel. Miami Laboratory, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami, FL 33149-1003. Contrib. Rep. MIA-93/94-42.

Several studies have examined spatial, temporal, and gear-related variation in life history and fishery parameters of king mackerel. The parameters have included mean back-calculated sizes, (Beaumariage, 1973; Manooch et al., 1987), von Bertalanffy growth rates (Johnson et al., 1983; Manooch et al., 1987), and size, age, and sex composition of the catch (Beaumariage, 1973; Johnson et al., 1983; Trent et al., 1983; Trent et al., 1987). The usefulness of this information for current stock assessments is limited for several reasons. Much of the previous work was based on data collected 15 to 25 years ago when exploitation was much lower, the species unmanaged, and population size, at least in the eastern Gulf of Mexico, higher. In addition, all age estimates were based on examination of whole otoliths, which results in considerable under-ageing of older, larger fish (Collins et al., 1989). In addition, some studies were geographically limited (Beaumariage, 1973; Trent et al., 1987), and because stock boundaries were unknown when the data were collected, none of the data were partitioned according to stock boundaries.

The primary objective of this study was to examine variation in age and growth in relation to space, time, and sex of king mackerel collected during 1977–78 and 1986–92.

Methods

Most king mackerel used in this study were collected during 1986–92 as part of a continuing cooperative program between the states from North Carolina to Texas and the National Marine Fisheries Service that was designed to provide age and length-frequency data needed to conduct annual stock assessments. Samples from 1977 and 1978 were collected by Johnson et al. (1983) for their age and growth study. All fish were measured to the nearest centimeter fork length (FL) and are reported in our study in those units.

Three regions, which reflect stock boundaries according to current hypotheses (Grimes et al., 1987; Johnson et al., 1994; Gulf of Mexico and South Atlantic Fishery Management Councils[3]), were sampled during 1986–92. The regions were 1) Atlantic: North Carolina to about Miami, FL; 2) eastern Gulf: Florida Keys through Mississippi, and, during April–October, Louisiana; and 3) western Gulf: Mexico, Texas, and, during November–March, Louisiana. All Louisiana samples were collected during April–October; therefore they were classified as eastern Gulf. We did not adjust the Atlantic–eastern Gulf boundary seasonally, as the current fishery management plan does, because only 378 of the 5,490 Atlantic fish aged were collected in the area of mixing off eastern Florida during November–March. These 378 fish were used in the analyses.

For the 1986–92 samples, taken from North Carolina to Yucatan, Mexico, we used stratified sampling (Ketchen, 1950), attempting to collect sagittal otoliths from 20 fish from each unique year, region, sex, and 10-cm size-interval combination. That quota was often exceeded for abundant size intervals and not reached for rarer size intervals.

The fish from Johnson et al.'s (1983) study were collected from recreational hook-and-line catches from North Carolina to Texas. Johnson et al. also used stratified sampling, with each sex and 10-cm size-interval combination comprising a stratum. For the analysis, regional classifications were the same as those used for the 1986–92 samples.

In most cases, heads were shipped to our laboratory where otoliths were removed and stored dry. The majority (>90%) of otoliths collected in the United States were taken from recreational hook-and-line catches, and the remainder from various commercial fisheries. All Mexican samples were collected from commercial fisheries.

For the 1986–92 samples, otoliths from males <80 cm and females <90 cm were read whole. The whole otoliths were placed in a black-bottomed dish containing glycerin and examined with a dissecting microscope at 12–25× with reflected light. For larger fish (males ≥80 cm and females ≥90 cm), three transverse sections about 0.7 mm thick were made about the focus with a Beuhler Isomet low-speed saw. Sections were mounted on glass slides with FLO-TEXX, a clear polymer mounting medium. Sections were examined under transmitted, polarized light at 50 or 125× with a compound microscope. Annuli of whole otoliths were identified according to the criteria of Johnson et al. (1983), and sections according to the criteria of Waltz.[5] The dorsal half of the section was usually read because it was clearer than the ventral. Otoliths collected during 1986–88 were read independently by two readers, and if there was disagreement, a second reading was made. If the second reading disagreed with the first, the otolith was excluded from analysis. After 1988, otoliths were read by the senior author alone.

Ageing methods for the 1977 and 1978 collections were basically the same, except that we sectioned males ≥75 cm and females ≥80 cm FL and used whole ages from Johnson et al. (1983) for fish below these sizes.

[5] Waltz, W. 1986. Data report on preliminary attempts to assess and monitor size, age, and reproductive status of king mackerel in the south Atlantic Bight. South Carolina Wildl. Mar. Res. Dep. MARMAP rep. for contract 6-35147.

Ages, to the nearest whole year, were assigned solely on the basis of number of visible annuli for fish collected from mid-July through December. Fish collected 1 January through mid-July had one year added to their age if the marginal increment was estimated to be >80% of the previous annual increment. Ages from samples collected by Johnson et al. (1983) were adjusted similarly with their marginal increment data. This adjustment was necessary because an annulus typically forms during the spring (Beaumariage, 1973; Johnson et al., 1983) but is often difficult to distinguish until later in the summer.

Von Bertalanffy growth equations were fitted to quarterly observed lengths-at-age by using Marquardt's nonlinear regression procedure (SAS Institute, Inc., 1988). Annual ages were converted to quarterly ages by adding 0.25 to the age if the fish was collected during April–June, 0.50 if collected during July–September, and 0.75 if collected during October–December. Quarterly ages were used to minimize the variance about the sizes-at-age because observed annual sizes-at-age, especially for young (1–2 yr old) fish that are growing faster than older fish, can vary considerably depending on month of capture.

For the 1986–92 data, we tested for differences in von Bertalanffy equations between sexes within regions and among regions within a sex, i.e. we compared fitted growth curves, using an F-statistic derived from the multivariate Hotelling's T^2 (Bernard, 1981; Vaughan and Helser, 1990). Estimates of the parameters L_∞, K, and t_0 are often correlated, making univariate statistical tests inappropriate for comparing differences between like parameters from two groups of fish (Bernard, 1981). To analyze the 1977–78 growth data, we simply examined plots of the von Bertalanffy curves and their 95% confidence limits. We did not use Hotelling's T^2 to test the 1986–92 data for interannual differences, the 1977–78 data for any growth differences, or to compare the 1977–78 and 1986–92 data, primarily because size and age distributions of the samples varied considerably among regions (and to some extent between sexes) and secondarily because the sample size was sometimes quite small. Von Bertalanffy parameter estimates, which are used as data for the Hotelling's T^2 test, would certainly be influenced by sample size and age distributions; if the two groups being tested had dissimilar distributions, then a significant difference might not be biologically meaningful.

Bernard (1981) noted that one of the assumptions for Hotelling's T^2 is that the two sets of estimates being compared have a common variance structure. However, citing Ito and Schull (1964), "if the variance-covariance matrices are unequal, the probability of a Type I error and correspondingly the power of the T^2 deviate from tabulated values with the same degrees of freedom. However, when both N_1 and N_2 are equal, different variance-covariance matrices do not effect the error level or the power of the test." To run each test with equal sample sizes so we could avoid the problems just mentioned, we randomly sampled from the larger group a number of observations equal to the sample size of the smaller group, then used parameter estimates derived from that sample in the test. However, all growth curves shown in the figures in the present study were based on the full number of available observations.

Results

We aged 14,213 king mackerel—12,180 collected during 1986–92, 2,033 from 1977–78. The numbers of females and males aged from 1986–92 were 3,407 and 2,083 from the Atlantic, 2,753 and 1,285 from the eastern Gulf, and 1,662 and 990 from the western Gulf. From the 1977–78 collections, the numbers of females and males aged were 323 and 128 from the Atlantic, 1,011 and 343 from the eastern Gulf, and 188 and 40 from the western Gulf (Table 1). The geographical distribution of the 1986–92 samples varied annually, and although fish were collected off every coastal state from Virginia to Texas and in Veracruz, Campeche, and in Yucatan, Mexico, the greatest proportion were collected in North Carolina in the Atlantic region, northwest Florida in the eastern Gulf, and south Texas in the western Gulf (Table 1). Most fish collected in 1977–78 came from North Carolina, northwest Florida, and Louisiana (Table 1).

Size and age distributions

Size distributions of aged fish were similar among regions during 1986–92, although females tended to predominate at larger sizes (Fig. 1). In contrast, in 1977–78, size distributions differed markedly, among both regions and sexes (Fig. 1). Males do not grow as large as females, and this difference was reflected in their narrower size distributions (Fig. 1; Table 2). Annual size distributions of aged fish, 1986–92, showed similar ranges each year but some variation in modal sizes (Table 2). The maximum sizes of females aged from 1986–92 were 152 (age 18 [yr]), 158 (age 18), and 147 (age 11) cm for the Atlantic, eastern Gulf, and western Gulf; sizes of males ranged to 121 (age 20), 127 (age 16), and 117 (age 13) cm for those same regions. Maximum sizes of 1977–78 samples were slightly smaller than those from 1986–92 in 5 out of 6 region and sex combinations, most likely because the older data had much smaller

Table 1

Geographical distribution of aged king mackerel for 1977–78, 1986–92, and each year from 1986 to 1992. N.E. Florida = Nassau-Flagler County. E. Florida = Volusia-Palm Beach County. S.E. Florida = Broward-Dade County. S. Florida = Monroe County. S.W. Florida = Sarasota-Collier County. W. Florida = Citrus-Manatee County. N.W. Florida = Escambia-Levy County. N. Texas = Jefferson-Calhoun County. S. Texas = Aransas-Cameron County.

		Number aged																	
		Females									Males								
Region	State or area	77–78	86–92	86	87	88	89	90	91	92	77–78	86–92	86	87	88	89	90	91	92
Atlantic Ocean	Virginia		20	—	—	—	16	1	—	3	—	3	—	—	—	1	1	—	1
	N. Carolina	234	1,982	64	134	68	313	454	402	547	71	1,239	59	101	37	255	274	230	
	S. Carolina	88	568	55	99	113	70	55	78	98	56	255	31	25	50	38	38	31	42
	Georgia	—	292	24	5	45	98	63	13	44	—	144	5	9	15	41	35	2	37
	N.E. Florida	—	52	21	31	—	—	—	—	—	—	6	5	1	—	—	—	—	—
	E. Florida	—	459	30	56	22	5	21	171	154	—	379	63	77	74	6	14	12	133
	S.E. Florida	—	34	6	15	10	3	—	—	—	—	57	14	20	23	—	—	—	—
Eastern Gulf	S. Florida	6	215	5	1	2	29	36	75	67	12	132	6	2	3	27	31	24	39
	S.W. Florida	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—
	W. Florida	—	110	2	—	—	—	—	—	108	—	14	2	2	—	—	—	—	10
	N.W. Florida	532	1,209	51	94	96	227	128	321	292	283	643	7	49	22	125	79	215	146
	Alabama	—	303	50	172	54	7	9	3	8	—	122	22	60	29	—	9	1	1
	Mississippi	7	290	31	55	51	6	69	47	31	—	104	7	8	31	4	26	12	16
	Louisiana	466	628	23	61	56	46	39	195	208	48	265	22	14	12	12	2	108	95
Western Gulf	Louisiana	147	1	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—
	N. Texas	41	281	—	45	90	54	14	47	31	38	181	4	27	56	30	14	23	27
	S. Texas	—	1,026	48	158	130	184	134	206	166	—	553	44	103	39	79	74	102	112
	Veracruz	—	225	—	—	6	47	75	50	47	—	183	—	—	9	44	31	53	46
	Campeche	—	21	—	—	—	13	8	—	—	—	16	—	—	—	7	9	—	—
	Yucatan	—	106	—	—	62	—	1	37	6	—	57	—	—	19	—	—	24	14

samples sizes and the sampling was more limited geographically and temporally.

During 1986–92, the overall age distributions of samples were quite similar among regions and between sexes within regions, but during 1977–78 they varied noticeably (Fig. 2). Maximum ages of king mackerel from 1986–92 in the Atlantic, eastern Gulf, and western Gulf were 26 (137 cm), 21 (127–150 cm), and 24 (144 cm) for females and 24 (117 cm), 22 (110 cm), and 23 (101 cm) for males. Maximum ages from 1977–78 samples from the same respective regions were 20, 19, and 18 for females and 18, 19, and 19 for males. Fish older than age 20 were very rare in the 1986–92 samples—only 22 of 7,822 females (0.15%) and 13 of 4,358 males (0.18%).

Growth

Growth was significantly different between sexes ($P<0.01$ in 1986–92) in each region during 1986–92 and 1977–78, and females grew faster and larger than males at every age (Fig. 3; Table 3). Although we did not test the 1977–78 data with Hotelling's T^2, it is obvious that the confidence limits do not overlap (Fig. 3). During 1986–92, the predicted sizes at age of females were at least 20 cm larger than males by age 13, 9, and 11 in the Atlantic, eastern Gulf, and western Gulf, respectively.

Age-at-size was highly variable in all regions for both sexes, especially after fish reached 70 cm FL (Tables 4 and 5). For example, Atlantic females 100.1 to 110.0 cm FL ranged from age 4 to 20, whereas males from that same region and size ranged from age 6 to 22.

The pooled 1986–92 data showed that growth was highest in the eastern Gulf, intermediate in the western Gulf, and lowest in the Atlantic for both sexes, and the differences, which were greatest among females, were statistically significant ($P<0.01$) (Fig. 3; Table 3). Asymptotic length (L_∞) was the parameter most often (7 of 9 instances) responsible for the significant differences between growth curves (Table 3), although twice it was t_0. Estimates of L_∞ were 126.7, 134.1, and 137.8 cm for Atlantic, western Gulf, and eastern Gulf females, and 96.4, 102.8, and 102.6 cm for males (Table 6). Above age 7 years, the predicted size at age of eastern Gulf

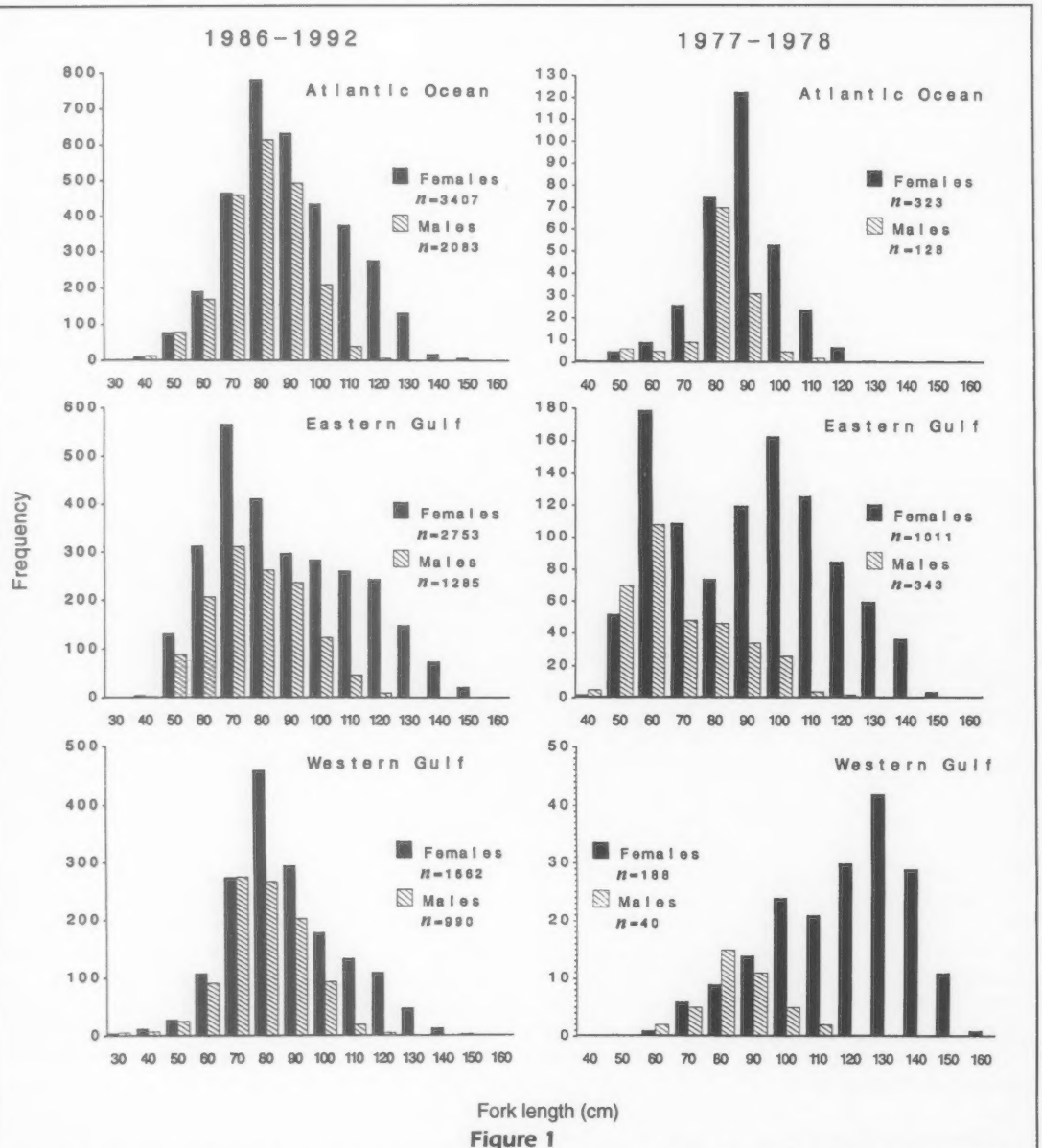

Figure 1

Length-frequency distribution by sex and region of king mackerel included in the analysis and collected during 1977–78 and 1986–92.

females averaged 12.2 cm (SD=0.4) larger than Atlantic females, whereas eastern Gulf males averaged 6.9 cm (SD=0.4) larger than Atlantic males.

The pattern of highest growth in the eastern Gulf, intermediate growth in the western Gulf, and lowest growth in the Atlantic seen in the pooled 1986–92 data was very consistent and present each year during that period. These consistent regional differences were especially noticeable among females (Fig. 4). Among males, the eastern Gulf growth curve was clearly higher than that for the Atlantic each year, whereas the growth curve for the western Gulf was intermediate in younger fish but converged with the eastern curve at about age 12–14 (Fig. 5).

In 1977 and 1978, as during 1986–92, growth of females was lowest for Atlantic fish; however, unlike

Table 2

Annual length frequency distributions of aged king mackerel, 1986–1992, by region and sex. See Figure 1 for overall 1977–78 and 1986–92 size distributions.

		Number aged													
	Size interval	Females							Males						
Region	FL (cm)	86	87	88	89	90	91	92	86	87	88	89	90	91	92
Atlantic	20–39.9	—	—	—	—	1	—	—	1	—	—	3	—	—	—
Ocean	40–59.9	23	72	7	14	14	16	17	36	50	12	5	27	20	13
	60–79.9	94	83	86	129	135	193	248	102	86	91	122	115	117	239
	80–99.9	57	83	91	205	230	289	315	35	88	87	195	186	107	217
	100–119.9	21	58	53	127	150	116	196	3	9	9	16	34	31	26
	120–139.9	5	42	21	30	57	50	67	—	—	—	—	—	—	1
	140–159.9	—	2	—	—	7	—	3	—	—	—	—	—	—	—
	Total	200	340	258	505	594	664	846	177	233	199	341	362	275	496
Eastern	20–39.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gulf	40–59.9	30	26	9	93	20	58	49	7	14	1	45	22	83	23
	60–79.9	50	135	94	79	99	242	267	20	69	37	58	60	128	170
	80–99.9	34	60	58	65	55	124	206	31	46	53	43	53	129	96
	100–119.9	30	73	55	39	66	153	133	8	11	5	22	11	20	17
	120–139.9	11	72	35	35	33	56	58	—	—	1	—	1	—	1
	140–159.9	7	17	8	4	6	8	1	—	—	—	—	—	—	—
	Total	162	383	259	315	279	641	714	66	140	97	168	147	360	307
Western	20–39.9	—	—	—	6	—	4	—	—	—	—	7	—	2	—
Gulf	40–59.9	—	3	11	12	14	8	29	—	3	8	9	11	6	35
	60–79.9	14	54	76	68	107	171	83	20	47	43	62	58	130	103
	80–99.9	19	88	101	124	70	108	104	27	69	65	64	53	56	57
	100–119.9	9	42	64	51	32	42	33	1	11	7	18	6	8	4
	120–139.9	6	15	36	32	10	7	2	—	—	—	—	—	—	—
	140–159.9	—	1	—	5	1	—	—	—	—	—	—	—	—	—
	Total	48	203	288	298	234	340	251	48	130	123	160	128	202	199

during 1986–92, western Gulf females grew faster and larger than eastern Gulf females according to the growth curves (Fig. 3). Among males, growth also appeared to be lowest in the Atlantic, although the differences were slight (Fig. 3).

There was interannual variation in growth within a region and sex during 1986–92; however, it probably reflected sample differences as much as any actual differences (Tables 1 and 2); therefore we did not test these growth curves statistically.

Plots of the von Bertalanffy curves (Fig. 6) suggested that growth was slightly less in 1977–78 than in 1986–92 in the Atlantic and eastern Gulf for both sexes, whereas western Gulf females grew faster in 1977–78 than in 1986–92. The average differences (and standard errors) in predicted size at age between 1986–92 and 1977–78 for all ages above age 7 were 1) eastern Gulf females: +2.0 ± 0.1 cm; 2) eastern Gulf males: +2.9 ± 0.1 cm; 3) Atlantic females: +5.8 ± 0.1 cm; 4) Atlantic males: +1.7 ± 0.1 cm; and 5) western Gulf females: –9.6 ± 0.6 cm.

Discussion

Our findings were based on data collected as part of a long-term, stratified, nonrandom sampling program (following the suggestions of Ketchen [1950]) designed to provide age-length keys for annual stock assessments. Most fish sampled were caught by hook and line and gill nets, both of which are size-selective gears. Goodyear (1995), using computer simulations, demonstrated that samples equally stratified by length and those from size-selective fisheries often yield biased estimates of mean size-at-age; for this reason he recommended that only simple random sampling be used to generate models of fish growth. He found that most often mean lengths-at-age were overestimated by 5–15% for all but the youngest age classes, which were sometimes underestimated. Goodyear explained that at the youngest ages, the smaller individuals of an age class are often sampled disproportionately to their true abundance, whereas for older ages, the same happens for

the larger (faster growing) fish in a given age class.

Given Goodyear's (1995) findings and our nonrandom sampling design, it may be that our growth models overestimated length-at-age to some degree for all but the youngest age classes, but probably not as much as Goodyear found in his study. Although we had sampling quotas for each year, region, sex, and 10-cm size interval combination, for many different reasons we invariably exceeded those quotas for all but the rarest size classes, often greatly for the most common length intervals; Table 2 and Figure 1 provide clear evidence of this. Because of this oversampling, our actual design fell somewhere between simple random sampling and length-stratified sampling, and thus should have reduced the bias to some extent. Given this rather small potential bias and the fact that our sample sizes and spatial and temporal coverages greatly exceeded all previous

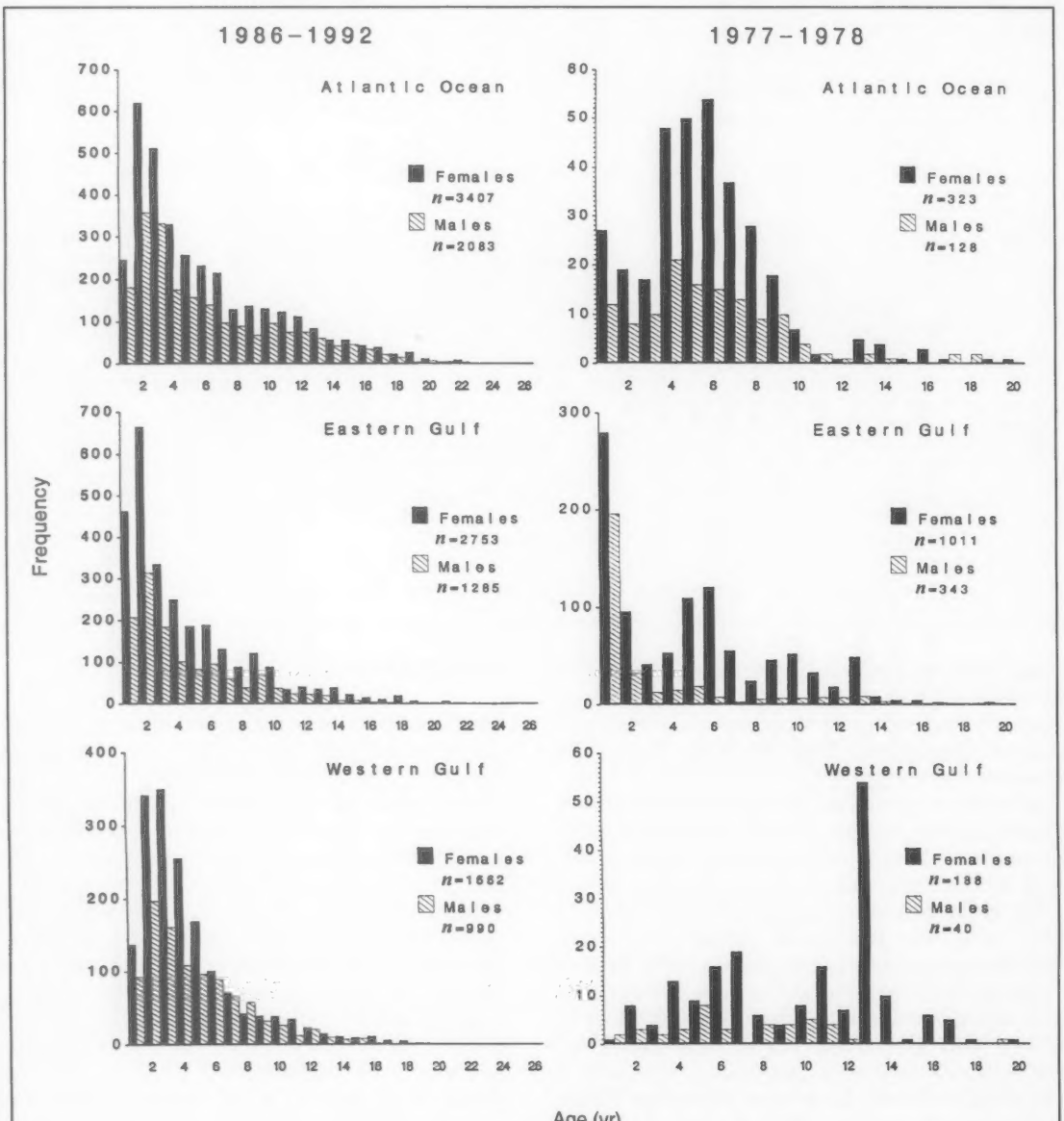

Figure 2

Age distributions by sex and region of king mackerel included in the analysis and collected during 1977–78 and 1986–92.

king mackerel studies (all of which sampled size-selective fisheries and only one (Beaumariage, 1973) of which clearly used simple random sampling), we feel our growth estimates are the best available. Most important, there is no obvious reason to suspect that the bias would be greatly different among regions or among years; thus our conclusions about the temporal and regional differences in growth should be valid.

Our finding of similar maximum longevity for both sexes differs from all previous studies (except

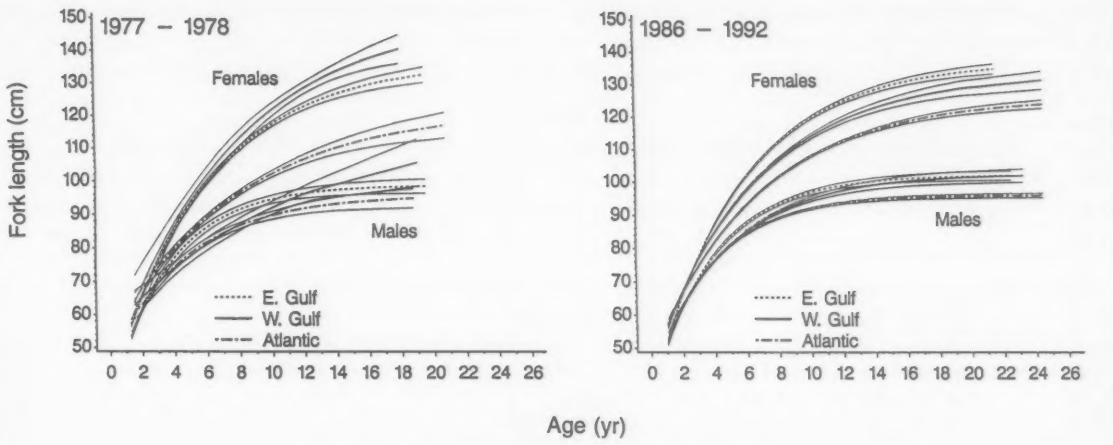

Figure 3

Von Bertalanffy growth curves and 95% confidence limits by region and sex for king mackerel collected during 1977–78 and 1986–92. Growth curves were calculated by using individual quarterly observed sizes-at-age. The upper three curves in each panel represent females; the lower three represent males.

Table 3

Results of Hotelling's T^2 tests comparing 1986–92 von Bertalanffy growth curves for king mackerel. The larger group in each comparison was randomly subsampled so that it's sample size equaled that of the smaller group. Underlined *F*'s in right three columns indicate parameters that did not significantly affect growth differences. Values in bold = parameter which most affected growth differences. NS = not significant. *n* = sample size for each group in the comparison. AOF = Atlantic Ocean females; EGF = eastern Gulf females; WGF = western Gulf females; AOM = Atlantic Ocean males; EGM = eastern Gulf males; WGM = western gulf males.

Groups compared	Calculated F[1]	*n*	Denom. df[2]	Critical value of *F* needed for 95% Roy-Bose simultaneous confidence limits to bracket zero		
				L_∞	K	t_0
AOF–EGF	363.8[2]	2,753	5,502	**28.4**	2.6	17.7
AOF–WGF	51.2	1,662	3,320	**3.2**	0.1	1.2
EGF–WGF	37.6	1,662	3,320	0.5	2.8	**8.2**
AOM–EGM	46.3	1,285	2,566	**16.5**	0.6	0.1
AOM–WGM	10.1	990	1,976	**9.8**	7.9	5.7
EGM–WGM	10.7	990	1,976	0.0	2.3	**4.0**
AOF–AOM	369.6	2,083	4,162	**211.8**	53.2	11.4
EGF–EGM	259.5	1,285	2,566	**133.3**	13.1	0.1
WGF–WGM	103.1	990	1,976	**46.2**	5.0	0.0

[1] Critical $F = 3.12$ ($\alpha = 0.05$, 2-tailed test) for all tests.
[2] Numerator df = 3 for all comparisons (3 parameters).

Beaumariage, 1973) that reported that females lived longer than males. The 26-year-old female and 24-year-old male we found are the oldest king mackerel reported. Collins et al. (1989), in the only other study that used sectioned otoliths, found a 21-year-old female as well as 16-year-old males. The oldest fish reported in all other studies that used whole otoliths, was age 14 for females and age 12 for males (Beaumariage, 1973; Johnson et al., 1983; Manooch et al., 1987; Sturm and Salter; 1990). Our findings support those of Collins et al. (1989), i.e. that sectioned sagittae provide higher age estimates than whole otoliths for king mackerel, especially for fish >85 cm FL. Among females ages 8–12 from the Johnson et al. (1983) study (the 1977–78 collections in our study), our age estimates based on sagittal

Table 4

Total age distributions by 10-cm length class, by region, for all female king mackerel collected during 1986–92.

Size (cm)	Age (yr)																							
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	24	*n*
Atlantic Ocean																									
35	25.0	50.0	25.0																						4
45	9.8	84.3	5.9																						51
55		65.1	34.9																						126
65		26.6	69.3	3.8	0.3																				290
75		5.0	41.0	40.7	11.2	1.8	0.4																		735
85		0.7	8.7	22.9	27.0	20.8	11.5	5.7	1.4	0.8	0.3	0.1	0.1												722
95			1.6	7.4	8.8	13.7	18.4	18.0	9.0	7.4	6.3	4.7	2.5	1.4	0.6	0.2									511
105					1.6	5.1	11.0	15.0	10.5	11.3	10.5	10.5	8.6	5.1	3.2	2.9	1.6	1.9	0.5	0.5	0.3				373
115						1.2	2.7	5.9	9.2	11.2	12.1	10.9	12.7	8.9	5.6	6.2	5.3	3.0	1.8	1.8	0.9		0.6		338
125							0.9	2.3	1.8	6.0	7.8	10.6	9.6	11.5	9.2	8.3	7.8	8.7	4.1	5.5	3.2	1.4	1.4		218
135								2.9		2.9	2.9		2.9	8.8	8.8	8.8	8.8	11.8	8.8	17.6	2.9		5.9	2.9[1]	34
145																42.9			14.3	14.3		14.3	14.3		7
155													25.0						50.0				25.0		4
Eastern Gulf																									
35	100.0																								4
45	12.5	87.5																							72
55		91.6	8.4																						249
65		34.1	58.8	6.6	0.4																				454
75		3.1	62.7	25.2	8.4	0.6																			512
85		0.3	16.7	43.4	24.4	7.7	3.9	2.6		0.3	0.3	0.3													311
95			1.8	13.7	31.7	23.2	16.9	4.6	1.8	3.5	1.4	0.7	0.4		0.4										284
105				0.7	11.3	22.5	24.5	13.9	8.9	9.9	5.0	0.3	0.7	1.0		0.3									302
115					1.7	8.4	16.0	22.3	13.0	16.0	11.3	4.6	1.3	1.7	0.8	1.3	1.3	0.4							238
125						2.2	8.6	8.1	11.8	15.1	17.2	6.5	10.8	6.5	5.9	2.7	0.5	0.5	2.2	0.5	0.5	0.5			186
135								0.9	2.8	13.2	7.5	3.8	14.2	11.3	12.3	9.4	4.7	6.6	9.4	1.9		1.9			106
145										2.3	2.3	9.1	2.3	11.4	22.7	9.1	11.4	4.5	9.1	6.8	2.3	6.8			44
155																25.0			50.0	25.0					4
Western Gulf																									
35		100.0																							10
45		91.7	8.3																						12
55	2.5	70.0	27.5																						80
65		35.1	51.0	9.9	4.0																				151
75		1.6	41.4	41.6	12.9	2.3	0.2																		442
85			15.2	33.0	29.6	15.7	4.7	0.8	0.8	0.3															382
95			0.5	11.2	27.1	28.5	16.8	9.3	2.8	1.4	0.9	0.9	0.5												214
105				0.6	12.2	15.4	21.8	19.2	10.9	7.1	6.4	3.8	0.6		0.6				0.6	0.6					156
115					1.7	10.3	8.5	12.0	10.3	12.8	13.7	11.1	9.4	4.3	0.9	0.9	1.7	0.9	1.7						117
125						2.9	2.9	4.3	4.3	12.9	7.1	12.9	12.9	10.0	8.6	8.6	7.1	2.9	1.4	1.4					70
135								4.2	4.2		16.7	16.7	4.2	12.5	12.5	8.3	16.7	4.2							24
145											16.7	16.7						33.3	16.7					16.7	6

[1] This size class also contained one fish (2.9%) at age 26.

sections exceeded their original estimates based on whole otoliths 67–100% of the time.

The slightly higher maximum ages in the Atlantic than in the eastern or western Gulf during 1986–92 may reflect lower fishing mortality rates for the Atlantic than for the Gulf where age structure was truncated by fishing pressure[4]; alternatively, this finding may be a sampling artifact. A much higher proportion of Atlantic samples were collected at fishing tournaments, which target larger and older fish, and Atlantic sample sizes exceeded eastern and western Gulf sample sizes by 36% and 107%; therefore the chances of obtaining an older fish were greater.

That females grew faster and attained larger maximum sizes than males agrees with previous studies (Beaumariage, 1973; Johnson et al., 1983; Manooch et al., 1987; Collins et al., 1989; Sturm and Salter 1990). The large variation in ages within size intervals that we found was also noted by Johnson et al. (1983).

Significant differences in growth among the three regions for both sexes during 1986–92 and the persistence of that pattern in each of the seven years support the hypothesis that there are three stocks as suggested by allozyme, mark-recapture, catch and fishing effort, and juvenile birth-date distribution data (Grimes et al., 1987; Johnson et al., 1994; Gulf of Mexico and South Atlantic Fishery Management Councils[3]). That similar differences between Atlantic and eastern Gulf growth were present in 1977–78 is further evidence that these growth differences

Table 5

Total age distributions by 10-cm length class, by region, for all male king mackerel collected during 1986–92.

Size (cm)	Age (yr)																						
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	*n*
Atlantic Ocean																									
35		100.0																							4
45		100.0																							58
55		61.6	37.6	0.8																					125
65		13.7	71.1	14.8	0.4																				263
75		0.8	19.3	43.0	21.8	10.0	2.7	1.1	0.6		0.3	0.2	0.2								0.2	0.2			632
85			0.4	3.5	6.3	16.8	20.7	12.4	10.9	7.6	7.6	5.4	5.0	0.9	0.9	1.1	0.2	0.2			0.2	0.2			542
95					0.3	0.9	2.3	5.8	6.4	7.3	13.1	11.3	11.0	13.1	8.1	7.8	5.8	2.9	2.6		0.3	0.6	0.3		344
105							3.1	3.1	4.1	2.0	7.1	5.1	7.1	11.2	10.2	11.2	10.2	9.2	6.1	4.1	3.1	2.0	1.0		98
115											6.2	6.2	12.5			12.5	18.8	12.5			6.2		12.5	6.2[1]	16
125																					100.0				1
Eastern Gulf																									
35																									
45	8.8	91.2																							57
55		74.8	25.2																						155
65		13.9	73.0	13.1																					267
75		0.7	27.8	43.7	19.0	6.0	1.8	0.7	0.4																284
85			0.4	8.4	15.1	24.4	26.1	9.2	5.0	8.0	2.1	0.4	0.8												238
95				1.5	4.5	4.0	11.9	14.9	9.5	18.4	12.4	6.0	8.5	5.0	1.5	1.0	0.5	0.5							201
105				1.6	3.1		4.7	7.8	7.8	17.2	9.4	17.2	4.7	10.9	4.7	3.1	1.6	3.1	1.6				1.6		64
115							4.8	9.5	4.8	14.3		4.8	9.5	4.8	9.5	19.0	4.8			9.5	4.8				21
125											33.3						33.3		33.3						3
Western Gulf																									
35	9.1	90.9																							11
45		85.7	14.3																						7
55		70.3	28.4	1.4																					74
65		9.3	56.5	29.0	5.2																				193
75		2.1	22.5	33.9	24.3	11.4	4.6	0.7	0.4																280
85			1.3	3.9	11.3	22.9	23.4	16.9	10.8	4.8	3.5	0.4	0.9												231
95					2.7	7.5	14.4	15.1	17.1	13.0	10.3	6.2	7.5	2.7	2.1	0.7				0.7					146
105							2.5	7.5	15.0	5.0	5.0	2.5	15.0	12.5	7.5	12.5	5.0		5.0	2.5				2.5	40
115									11.1		11.1	11.1	22.2	11.1	11.1	22.2									9

[1] This size class also contained one fish (6.2%) at age 24.

are consistent features of king mackerel populations. Assuming that these differences persisted from 1977 to 1992, during which time exploitation rates varied considerably (Mackerel Stock Assessment Panel[4]), we suggest that these differences are not just temporary density-dependent responses to varying population sizes or exploitation rates.

Our findings of regional (stock) growth differences are also consistent with those of Gold et al. (in press), who compared mtDNA haplotypes and found weak genetic differences between Atlantic and Gulf king mackerel. Although our results are not indicative of genetic discontinuity, our data demonstrate that the three groups of fish experience sufficiently different environmental and fishery conditions to produce identifiable and consistent differences in growth.

Contrary to our finding of regional differences in growth within sexes, Beaumariage (1973) reported that growth rates did not differ for either sex between the Gulf and Atlantic coasts of Florida. His results may reflect that many of his Atlantic fish were collected off southeast Florida during winter and thus may have been Gulf-group fish. In addition, the use of whole otoliths for ageing undoubtedly introduced error in length-at-age estimates, possibly obscuring regional differences.

Johnson et al. (1983) reported that female king mackerel from Louisiana grew faster than females from other areas of the Gulf and from the Atlantic. However, their predicted sizes-at-age for Louisiana females ages 4–8, the ages with adequate sample sizes (n=16–78) that could be accurately aged with whole otoliths, were no more than 3.1 cm different from our eastern Gulf fish. For fish older than age 8, their estimates were increasingly larger than ours, most likely because the use of whole otoliths resulted in underageing these larger fish.

The growth differences between 1977–78 and 1986–92, i.e. lower growth during the former period seen in both sexes in the Atlantic and eastern Gulf (Fig. 6), could be a density-dependent response. Populations were much larger in the late 1970's and early 1980's than during 1986–92 (Mackerel Stock Assessment Panel[4]). The key point to remember is that within sexes, the growth differences among regions clearly present in 1986–92 apparently existed as far back as 1977–78.

Acknowledgments

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Table 6

Von Bertalanffy parameters and 95% asymptotic confidence intervals for male and female king mackerel by region for fish collected during 1986–92 and 1977–78, calculated using quarterly observed sizes-at-age.

			Females			Males		
Collection years		Parameter	n	Estimate	Asymptotic 95% confidence interval	n	Estimate	Asymptotic 95% confidence interval
1986–92	Atlantic	L_∞	3,407	126.7	125.0 to 128.5	2,083	96.4	95.7 to 97.1
	E. Gulf	L_∞	2,796	137.8	135.8 to 139.8	1,330	102.6	101.1 to 104.1
	W. Gulf	L_∞	1,662	134.1	130.6 to 137.7	995	102.8	100.5 to 105.2
	Atlantic	K	3,407	0.145	0.137 to 0.154	2,083	0.262	0.248 to 0.276
	E. Gulf	K	2,796	0.172	0.163 to 0.181	1,330	0.247	0.227 to 0.267
	W. Gulf	K	1,662	0.150	0.136 to 0.164	995	0.203	0.180 to 0.226
	Atlantic	t_0	3,407	–3.15	–3.41 to –2.90	2,083	–1.98	–2.19 to –1.78
	E. Gulf	t_0	2,796	–1.83	–1.98 to –1.67	1,330	–1.84	–2.09 to –1.59
	W. Gulf	t_0	1,662	–2.69	–3.02 to –2.37	995	–2.74	–3.16 to –2.32
1977–78	Atlantic	L_∞	323	122.7	115.5 to 129.9	128	95.9	92.3 to 99.6
	E. Gulf	L_∞	1,011	137.1	133.4 to 140.8	343	99.0	96.6 to 101.3
	W. Gulf	L_∞	188	151.5	138.2 to 164.8	40	116.0	93.1 to 138.9
	Atlantic	K	323	0.124	0.096 to 0.151	128	0.211	0.159 to 0.262
	E. Gulf	K	1,011	0.160	0.145 to 0.175	343	0.269	0.229 to 0.309
	W. Gulf	K	188	0.127	0.080 to 0.175	40	0.094	0.026 to 0.163
	Atlantic	t_0	323	–4.54	–5.59 to –3.49	128	–3.14	–4.26 to –2.02
	E. Gulf	t_0	1,011	–2.12	–2.39 to –1.85	343	–1.63	–2.04 to –1.22
	W. Gulf	t_0	188	–2.78	–4.52 to –1.03	40	–6.78	–11.1 to –2.45

colleagues at the Mote Marine Laboratory were especially helpful both in field sampling in Mexico and in ensuring the shipment of samples and data to us. Special thanks are also due to the North Carolina Division of Marine Fisheries and, in particular, to L. Mercer, L. Nobles, and R. Gregory, for providing us

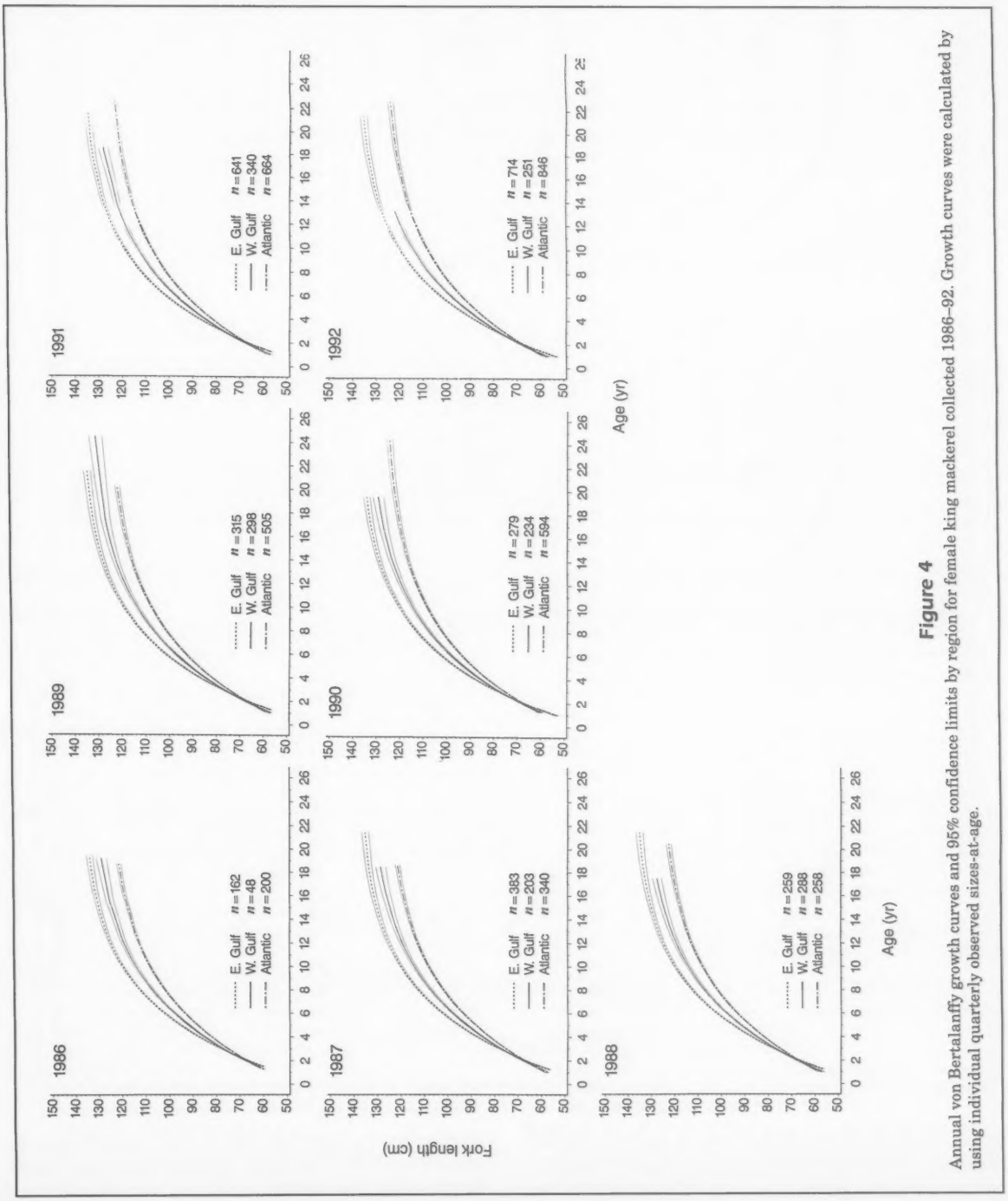

Figure 4

Annual von Bertalanffy growth curves and 95% confidence limits by region for female king mackerel collected 1986–92. Growth curves were calculated by using individual quarterly observed sizes-at-age.

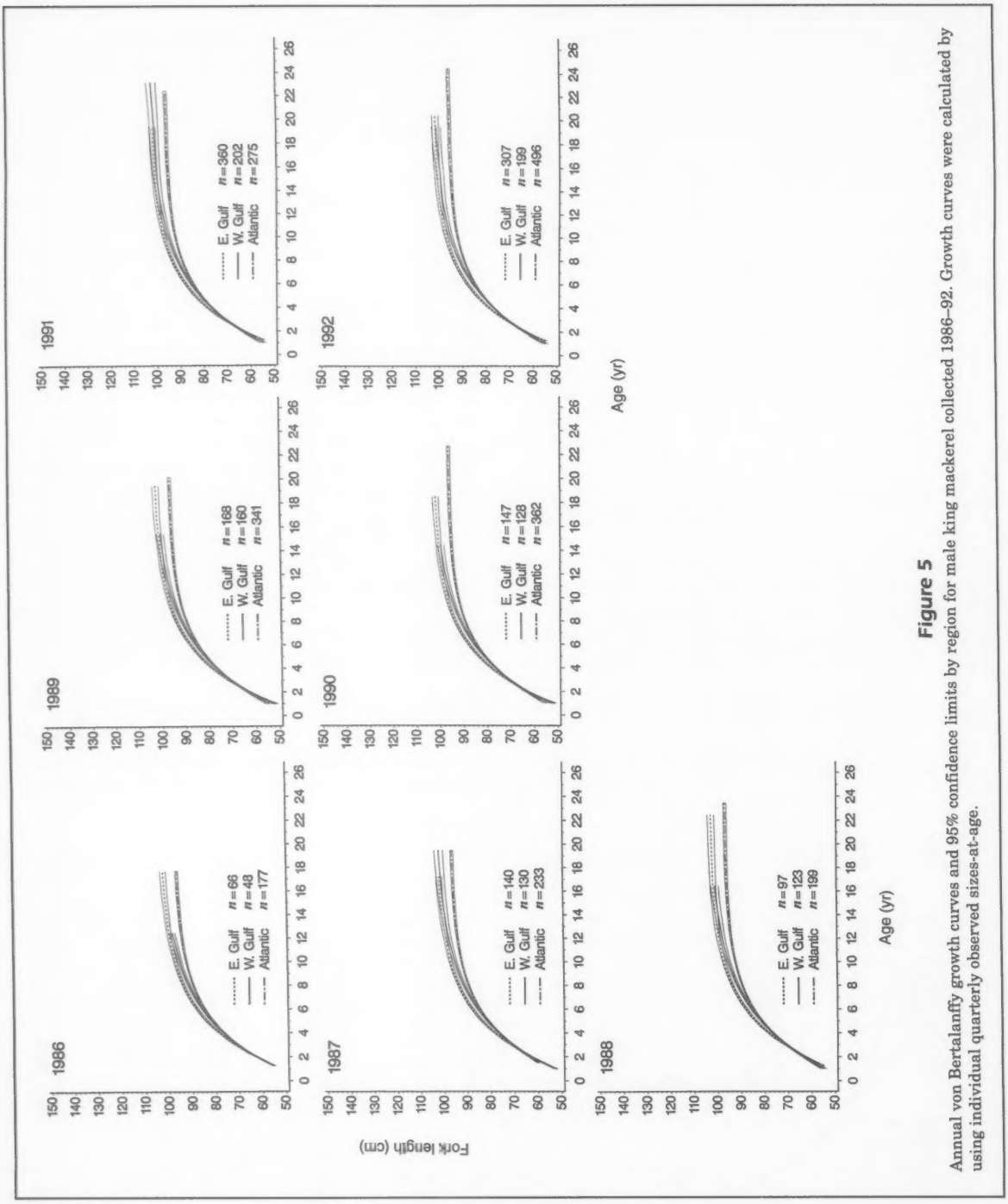

Figure 5

Annual von Bertalanffy growth curves and 95% confidence limits by region for male king mackerel collected 1986–92. Growth curves were calculated by using individual quarterly observed sizes-at-age.

with large numbers of processed otoliths. Doug Vaughan, NMFS, Beaufort Laboratory, provided programs and valuable statistical advice concerning comparisons of growth curves. Two anonymous reviewers provided valuable suggestions that helped improve the manuscript.

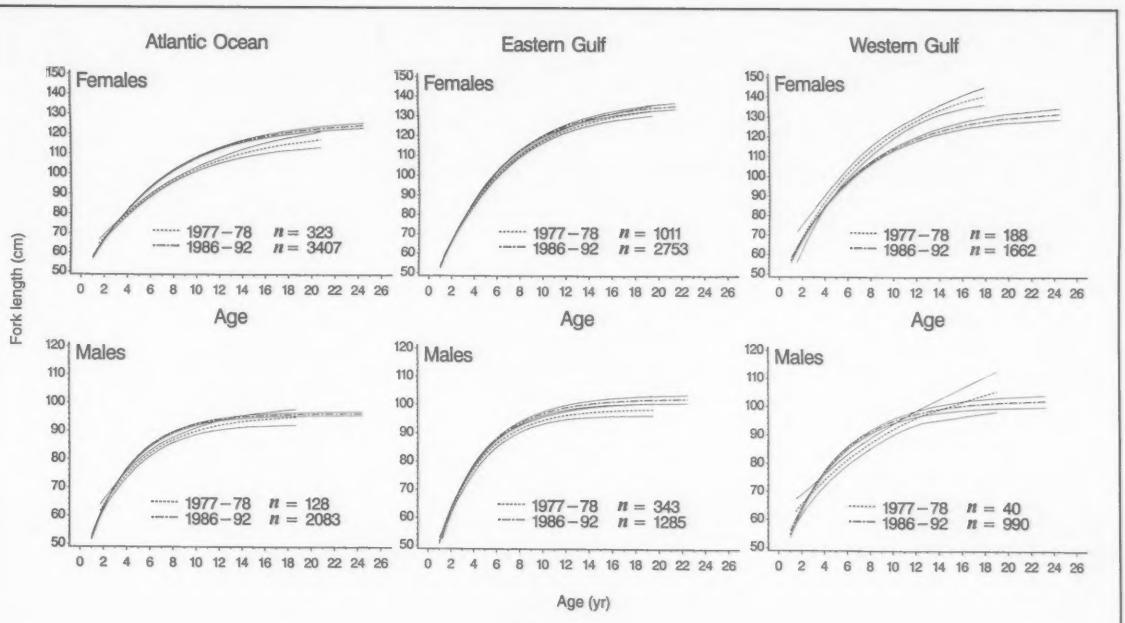

Figure 6

Overall von Bertalanffy growth curves and 95% confidence limits by region and sex for king mackerel, from 1977–78 and 1986–92. Curves were calculated by using quarterly observed size-at-age.

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Age, growth, distribution, and food habits of recently settled white seabass, *Atractoscion nobilis*, off San Diego County, California

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Abstract.—White seabass, *Atractoscion nobilis*, is a valuable recreational and commercial species, but much of its early life history is undescribed. The coast and two bays of San Diego County were sampled each month for two years with a depth-stratified sampling design to determine habitat, food habits, age, and growth rate of recently settled fish. Age was estimated from otolith increments and validated with fish of known age, reared in the laboratory. A few recently settled fish were caught in the bays at depths <1 m, but most inhabited shallow water (4–8 m) along the coast from May to October. This depth distribution coincides with that of the mysid *Metamysidopsis elongata*. Fish abundance in this zone was low, however, reaching a maximum of 24/ha in July. The smallest white seabass collected were about 7 mm SL and 26 d old, but previous studies indicate that smaller and presumably younger fish were probably extruded through the trawl. According to combined results, most larvae settled 2–3 weeks after being spawned. Juveniles remained at a depth of 4–8 m for 2–3 months, fed primarily on abundant mysids, and associated with drifting macrophytes (r=0.52, P=0.015, n=21). Growth during this period was 1.3 mm/d, similar to that observed in the laboratory. At about 100 mm SL (~100 d old), juveniles appeared to move out of the area. The shallow waters just beyond the breaking waves may be preferred by young white seabass because abundant food and warm water promote rapid growth and drifting macrophytes provide a refuge from predators.

Manuscipt accepted 30 May 1997.
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White seabass, *Atractoscion nobilis* (family Sciaenidae), is a highly desired recreational and commercial species found in waters off the coasts of southern and Baja California as well as in the Gulf of California. Adults inhabit the nearshore zone over rocky bottoms and in kelp beds and can attain a weight of 38 kg (Young, 1973). Population size has not been estimated, but since the 1920's, commercial and recreational landings off California have continued to decline and the range of the species has contracted (Collins, 1981; Methot, 1983). Management efforts to stabilize and restore the population have been largely unsuccessful. Reductions in the catch and distribution of white seabass have been attributed largely to overfishing (Thomas, 1968; Vokovich and Reed, 1983; MacCall, 1986), but the importance of other mechanisms, such as increased natural mortality of fish at early life history stages, has not been evaluated.

Despite the historic value of this species, much of its early life history was unknown until recently. Moser et al. (1983) described the development of the early life stages and historic distribution of larvae in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling area off southern and Baja California. In several laboratory studies, growth, survival, energetics, and feeding behavior of larvae have been examined (Kim, 1987; Dutton, 1989; Orhun, 1989), as well as the development of sensory systems and predator-avoidance behavior (Margulies, 1989).

Less is known about the early juvenile stage because few early juveniles have been caught until recently. Early studies suggested that juveniles inhabit either the surf zone or kelp canopy along the open coast, or bays and estuaries (Thomas, 1968; Feder et al., 1974; Maxwell[1]). Allen and Franklin (1988, 1992) have since demonstrated that late larvae and early juveniles inhabit shallow water along the open coast of southern California and Channel Islands and semiprotected embayments in the vicinity of Long Beach Harbor. However the nursery area for white seabass has not been clearly defined and the relative importance of the open coast and bays as nurseries has not been

[1] Maxwell, W. D. 1977. Progress report of research on white seabass, *Cynoscion nobilis*. Calif. Dep. Fish Game, Mar. Resour. Admin. Rep. 77-14, 14 p. [Available from Calif. Dep. Fish Game, 330 Golden Shore, Suite 50, Long Beach, CA 90802.]

evaluated. In addition, food habits, age, and growth of these fish in the wild have not been examined.

The specific goals of this study were to determine 1) the depth distribution of early juvenile white seabass along the open coast and in bays of San Diego County, 2) size-specific food habits of white seabass, and 3) age and rate of growth.

Materials and methods

Sampling design

Most white seabass were obtained from a survey originally designed to sample settled California halibut, *Paralichthys californicus* (Kramer, 1990). Two bays (Mission Bay and Agua Hedionda Lagoon) and the open coast of San Diego County were sampled monthly from September 1986 to September 1988 with a depth-stratified sampling design. The coast was sampled at four primary sites with a 1.6 m × 0.35 m beam trawl (Fig. 1). At each site, four benthic tows were made in each of three bottom depth intervals (strata): 4–8, 9–11, and 12–14 m. A few tows were made in water as shallow as 3 m on days when the sea was calm. Tows were made parallel to shore at about 0.6 m/s for 10 min. The exact depth of tows within each stratum was chosen at random. Sampling depth was maintained along the chosen 1-m depth contour with the aid of a fathometer. An odometer attached to the trawl recorded tow distance, which ranged from 250 to 450 m. An additional four sites were sampled from April to October 1988 by biologists at San Diego State University (SDSU) with identical gear, but only at the 4–8 and 9–11 m depth strata.

A similar sampling design was used to sample the two bays. Mission Bay and Agua Hedionda Lagoon were subdivided into five and three blocks respectively to sample the various habitats adequately within each bay (Fig. 1). Each block was further subdivided into three depth strata: 0–1, 1–2, and 2–4 m. Within each stratum and block, three benthic tows were made at random locations with a 1.0 m × 0.35 m beam trawl equipped with an odometer. In the two deeper strata, the trawl was towed by a 5-m skiff for 5 min, covering a distance of 100–250 m. In the 0–1 m stratum, the trawl was towed by hand for a measured distance of 20–50 m. The 0–1 m depth stra-

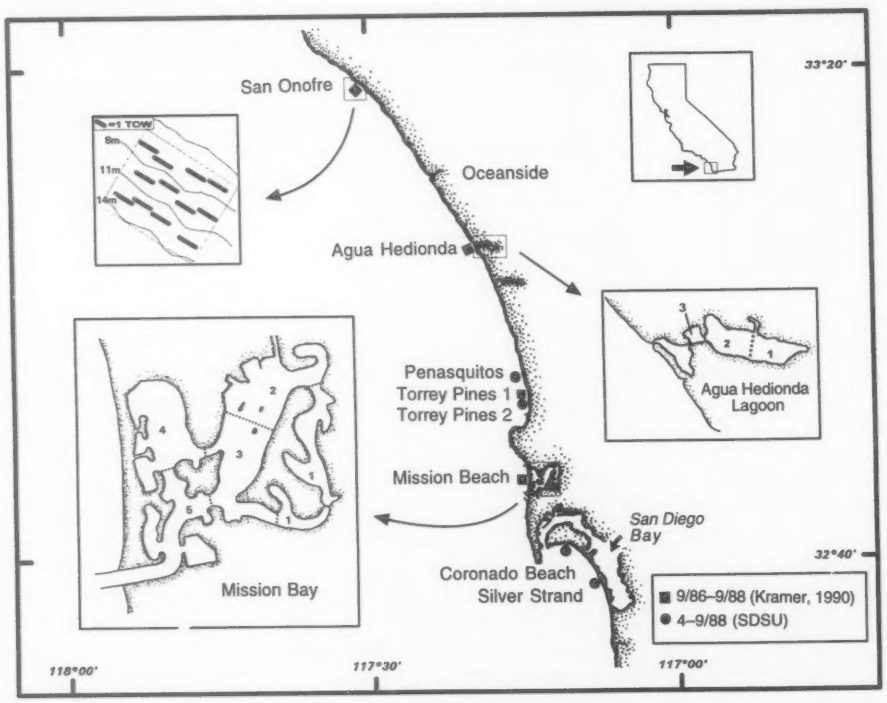

Figure 1

Map of San Diego County showing location of the eight coastal sites and sampling areas (blocks) within Mission Bay and Agua Hedionda Lagoon. Four coastal sites were sampled by Kramer (1990) and four were sampled by San Diego State University (SDSU). The sampling design used along the coast is also shown.

tum was also sampled with a 1 m × 6 m beach seine. Three hauls were made in each block over a measured distance of 15–50 m with the width of the seine fixed at 4 m. In addition, three tows were made each month in blocks 2–5 of the 2–4 m stratum in Mission Bay with the 1.6-m beam trawl (Fig. 1). The mesh size of all three nets was 3 mm. All hauls were made during the day. Monthly sampling in Agua Hedionda Lagoon was not initiated until March 1987.

Tow distance, water temperature, and the presence and type of drift macrophytes in the net were recorded at the end of every tow. Beginning in April 1988, the weight of drift macrophytes in each tow was also recorded at the four coastal sites sampled by SDSU biologists. White seabass were either frozen or preserved in 80% ethanol and later measured to 0.1 mm standard length (SL) in the laboratory. Lengths of alcohol-preserved fish were adjusted by 3.6% to compensate for shrinkage. Average shrinkage was estimated by measuring a subsample of white seabass before and several months after preservation in ethanol. Sagittae and stomach contents were removed and stored in 80% ethanol. Fish were then dried at 60°C for two days and weighed.

White seabass were also obtained opportunistically (i.e. sporadically) from the coastal habitat with a 7.6-m headrope otter trawl and a 15.2-m beach seine (6-mm mesh). These fish were used only in the food habits and growth portions of this study.

Distribution and abundance

Abundance was calculated as the number of fish caught divided by the product of tow distance (from odometers) and net width. Mean abundance of fish along the coast was calculated for each site by depth stratum (n=4 tows). Monthly differences in abundance among the three depth strata were compared by using the Kruskal-Wallis test, with a=3 depths, and n=4 (1987) or n=8 (1988) sites (Sokal and Rohlf, 1981). Monthly mean abundance in bays was calculated for each bay by block and depth stratum. Block means were averaged to produce a mean for each bay and the two bays were averaged to yield a grand mean for each depth stratum. Because estimates of monthly mean abundance did not differ among the two gear types (paired t-test; mean difference=0.50 fish/ha, t=0.27, df=8, P=0.79), trawl and seine samples within the 0–1 m depth stratum were pooled to produce an improved estimate of abundance.

The relation between abundance of white seabass and drift macrophytes was estimated by testing for a correlation between abundance of white seabass and drift macrophytes in each tow and for a correlation between mean abundances at each site (n=4 tows). Abundance of macrophytes (g/m^2) was log-transformed prior to analysis. Biomass of macrophytes was recorded only from April to October 1988 at the four secondary sites along the coast that were sampled by SDSU biologists.

Food habits

The stomach contents of 142 white seabass collected in bays and along the coast with all gear types were examined. For each fish, prey items were identified, counted, sorted into one of ten major prey categories, dried at 60°C for 1–2 d, and weighed to either 1 µg (for samples <25 mg) or to 0.1 mg (for samples >25 mg). White seabass were grouped into six length classes: 6–10, 10–18, 18–25, 25–35, 35–55, and 55–150 mm SL. Class intervals were chosen so that each interval contained similar numbers of fish. Mean prey weight and frequency of occurrence of each prey category were calculated for the six length classes. Six individuals with empty stomachs were excluded from calculations of frequency of occurrence and mean weight of prey.

Age and growth

The ageing method was validated by using laboratory-reared fish of known age. Eggs obtained from captive broodstock were placed in 7-m^3 flow-through tanks and reared at 17–20°C on a diet of marine rotifers, brine shrimp, euphausids, and chopped mackerel. White seabass were sacrificed at irregular intervals between 13 and 76 d after hatching and stored in 80% ethanol. Sagittae were mounted in Eukitt mounting media and ground in the sagittal plane with 15-µm grit sandpaper and polished with 0.3-µm grit lapping film. Increments were counted on the right sagitta from the central primordium to the mid-ventral margin. Each sagitta was read in one session by one observer, with neither age nor length of the fish known to the reader. The rate of increment deposition and age at first increment formation were estimated by linear regression.

A subsample of 50 wild larval and juvenile white seabass was aged with the technique described above. Individuals were selected at random from several length classes to represent equally the size range of fish collected. The subsample included fish caught in bays, on the coast, and in both years. Growth rates were estimated by fitting a Gompertz function ($L_t = L_0 e^{G(1-e^{-gt})}$) to length-at-age and weight-at-age data. The ages of the remaining individuals were estimated from the resulting age-length relation. The date each fish was spawned was calculated by subtracting the age of the fish and an additional two days (incubation time at ~16°C; Orhun, 1989) from date of cap-

ture. The error associated with the estimated spawn dates is therefore the same as that associated with the age-length relation.

Growth of wild white seabass was compared with growth of three groups reared in the laboratory. Eggs spawned on 8 May, 24 June, and 25 September 1989 were reared as described above. Mean length-at-age was estimated from random subsamples (n=16–76 fish) taken at irregular intervals during rearing. Linear growth models were fitted to the length-at-age data for both reared and wild fish to facilitate statistical comparisons of growth rates with ANCOVA. Although growth of white seabass from hatching to 150 mm SL was nonlinear, growth over a smaller size range of 6–104 mm SL was described equally well by linear models ($r^2 \geq 0.94$).

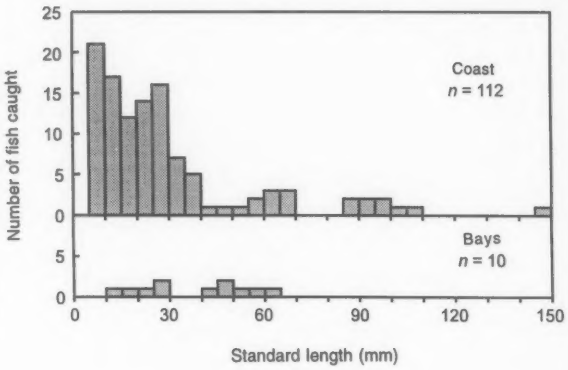

Figure 2

Length-frequency distributions of white seabass caught during regular sampling along the coast of San Diego County with a 1.6-m beam trawl and in Mission Bay and Agua Hedionda Lagoon with 1.6-m and 1.0-m beam trawls and a 6-m beach seine.

Results

Distribution and abundance

The overall abundance of white seabass in the bays and along the coast of San Diego County was low. During regular sampling, a total of 112 white seabass were caught in 1,250 tows along the coast and 10 white seabass were caught in 2,527 tows in the bays. Most tows caught no white seabass. Lengths of fish ranged from 6.2 to 149 mm SL (x= 30.2 mm SL), but 80% were smaller than 40 mm SL (Fig. 2). About 40 fish (33%) were smaller than 15 mm SL, the approximate length at metamorphosis (Moser et al., 1983).

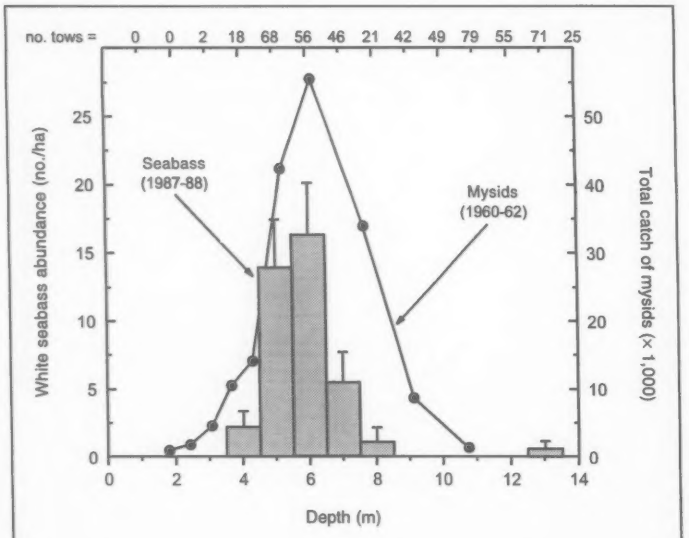
no. tows = 0 0 2 18 68 56 46 21 42 49 79 55 71 25
White seabass abundance (no./ha)
Seabass
(1987-88)
Mysids
(1960-62)
Total catch of mysids (× 1,000)
Depth (m)

Figure 3

Distribution of white seabass and the mysid *Metamysidopsis elongata* along the coast in relation to depth. White seabass abundance is the mean (± 1 SE) during months fish were captured (Jun–Aug 1987, May–Oct 1988). Number of tows at each depth during this period is indicated at the top of the graph. Mysid data are redrawn from Clutter (1967) and represent total number of *M. elongata* caught from 1960 to 1962 at a site ~3 km south of the Torrey Pines 2 site (Fig. 1). Sampling effort for mysids was similar for all depths.

White seabass were caught primarily in shallow water in both coastal and bay habitats. Along the coast, nearly all white seabass (97%) were collected in the shallowest (4–8 m) depth stratum, with the highest density at 6 m (Fig. 3). Only three fish were taken in deeper water and these were among the largest caught, ranging from 92 to 149 mm SL. In the bays, all ten fish were caught in the shallowest (0–1 m) stratum.

Settled (demersal) white seabass were present in shallow strata only during spring and summer, although one fish, the 149-mm-SL juvenile, was caught in January 1988. Along the coast, white seabass were caught from June to August 1987, and from May to October 1988, when sampling ended (Fig. 4). In both years, abundance was highest in July, with mean densities of 15/ha (1987) and 24/ha (1988). White seabass were found in 54 of 210 tows (26%) made in the 4–8 m

stratum during these nine months. Because most tows in the 4–8 stratum caught no white seabass, the variance associated with the estimates of abundance within the stratum was high. As a result, abundance in the 4–8 m stratum did not differ statistically from that in the 9–11 and 12–14 m strata (generally zero) except in June 1987 and from June to July 1988 (Kruskal-Wallis test, $P<0.05$, $n=4$ or 8). The temperature in the 4–8 m stratum during the summer ranged from 16 to 20°C, an average of 1.2 and 1.8°C warmer than the two deeper strata.

Although the relative abundance of settled white seabass was lower in the bays than along the coast, the two estimates could not be compared statistically because different nets were used to sample the two habitats. In addition, only 10 fish were caught in the two bays, making estimates of abundance sensitive to capture of individual fish. Estimates of mean density in the 0–1 m stratum in the bays from April to August ranged from 0 to 5 per ha in 1987 and from 0 to 10 per ha in 1988 (Fig. 4). The high April 1988 estimate resulted from a single fish caught in a short tow. Mean abundance during these five months (total catch ÷ total area swept) was 1.3/ha in 1987 and 3.1/ha in 1988. Monthly estimates for bays were about 0.8–12 times lower than estimates for the coast during the same period.

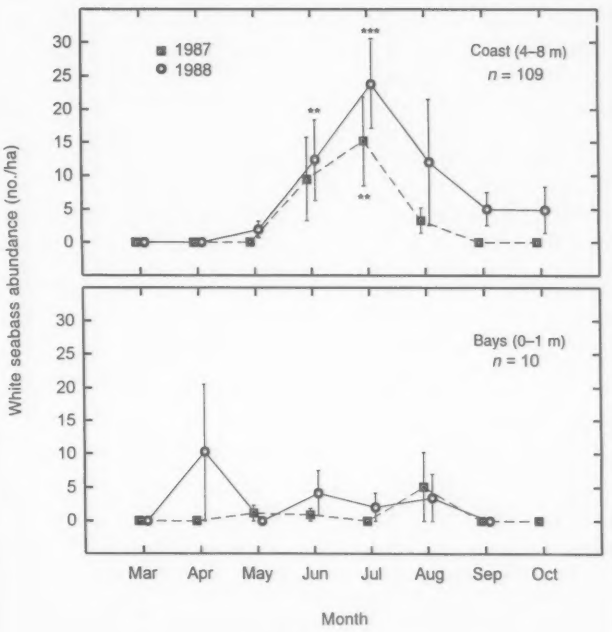

Figure 4

Monthly mean abundance of white seabass (± 1 SE) in the 4–8 m stratum along the coast (1987 $n=4$ sites; 1988 $n=8$ sites) and in the 0–1 m stratum in the bays ($n=2$ bays). Means that are significantly different from those in the 9–11 and 12–14 m strata (usually zero—not shown) are indicated (Kruskal-Wallis test, ** = $P\leq0.01$; *** = $P\leq0.001$).

Abundance of white seabass within the 4–8 m coastal stratum was related to the abundance of drift macrophytes. Drift macrophytes were common in the 4–8 m stratum and were recorded in 188 of 205 tows (92%) made during the nine months when white seabass were present. Macrophytes were present in 49 of 52 tows (94%) that caught white seabass. The drift material was mainly giant kelp (*Macrocystis pyrifera*) and surf grass (*Phyllospadix torreyi*), but filamentous red and other brown algae were dominant at times. In 1988, weight of macrophytes in each tow was recorded at the four sites sampled by SDSU biologists. At these sites, abundance of white seabass in each tow was weakly correlated with the abundance of drift macrophytes in each tow in the 4–8 m coastal stratum ($n=77$, $r=0.29$, $P=0.01$, Fig. 5A). Because white seabass were not abundant, an average of the four tows made at each site was also calculated. Mean abundance of white seabass at each site ($n=4$ tows) and mean abundance of drift macrophytes were more strongly correlated ($n=21$, $r=0.52$, $P=0.015$, Fig. 5B). Drift macrophytes were also present in the two deeper strata, but only three white seabass were caught at those depths.

Food habits

Along the coast, white seabass of all length classes fed almost exclusively on mysid crustaceans. For each length class, mysids composed from 74% to 99% of the diet by weight and were found in 78–100% of stomachs that contained food (Table 1). These mysids were not identified to species but were probably *Metamysidopsis elongata*, the numerically dominant mysid in the nearshore coastal habitat (Clutter, 1967; Roberts et al., 1982). Larger white seabass ate larger mysids, although fish >0.2 g dry weight (~40 mm SL) fed on mysids of similar mean weight (Fig. 6). Mysids also dominated the diet of the 10 fish caught in the bays.

Prey of secondary importance varied with white seabass length class. Larvae (6–10 mm SL) fed on copepods, fish of intermediate length (10–55 mm SL) fed on gammarid amphipods, and larger juveniles

(35–150 mm SL) preyed on shrimp and fishes. Most fish in the stomachs were well digested and difficult to identify, but the sagittae closely resembled those of white croaker, *Genyonemus lineatus*, and queenfish, *Seriphus politus*. One case of cannibalism was observed; a 7-mm larva was eaten by a 35-mm juvenile. Most shrimp were well digested, but at least two individuals were identified as belonging to the genus *Crangon*. Other items found in the stomachs included nematodes, bits of algae and surf grass, portions of crustaceans, and sand. The stomachs of six white seabass (5%) were empty or contained only nonfood items such as sand.

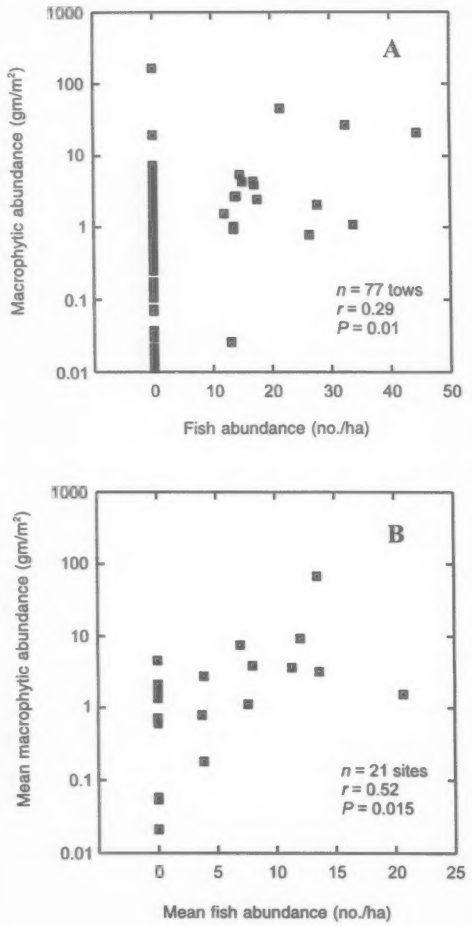

Figure 5

Relations between (**A**) abundance of drift macrophytes and abundance of white seabass in each tow, and (**B**) mean abundance of drift macrophytes and mean abundance of white seabass at each site (n=4 tows) in the 4–8 m stratum from April to October 1988 at the four coastal sites sampled by SDSU. Sample size, Pearson correlation coefficient (r), and P-values are shown.

Age and growth

Otolith increments formed daily in sagittae of laboratory-reared white seabass (Fig. 7). The slope of the regression of observed number of increments on age was 0.96 and did not differ from unity (r^2=0.96, n=25, P<0.01, 95% confidence limits on slope: 0.89 and 1.04 increments/d). The first increment formed 3–4 d after hatching, a period that corresponds to yolk absorption and onset of feeding (Kim, 1987; Orhun, 1989).

Age was estimated for 50 wild white seabass ranging from 6.2 to 104 mm SL. The ten smallest fish that were aged ranged from 6.2 to 9.2 mm SL and were estimated to be 26–32 d old (Fig. 8). The age of a fish that was 15 mm SL, the length at metamorphosis, was estimated to be about 40 d. The largest juvenile aged (104 mm SL) was estimated to be 108 d old. The range of estimated ages suggests that white seabass remain in the nursery for 2–3 months after settlement. It should be noted that the oldest validated age was 76 d. A 149-mm-SL juvenile was not aged because it was probably much older than the oldest validated age.

Growth of these fish was rapid in terms of length and weight. The parameters of the Gompertz model relating age and length were estimated as L_0=0.202, G=6.64, and g=0.0273, where L_0 is length at time t_0, G is the instantaneous growth rate at time t_0, and g is the rate of decrease of G (Fig. 8A). This equates to a maximum growth rate of 1.57 mm/d at 70 d. Weight also increased rapidly. The parameters relating weight and age were $W_0=2.72 \times 10^{-7}$, G=17.58, and g=0.0256, where W_0 is weight at time t_0 (Fig. 8B).

Wild fish between 6 and 104 mm SL grew at rates similar to those of laboratory-reared fish. Wild fish grew at a linear rate of 1.31 mm/d, compared with laboratory rates of 1.15, 1.32, and 1.04 mm/d for groups spawned in May, June, and September 1989 (Fig. 9). Linear growth models were used to facilitate statistical analysis by ANCOVA. Linear models fitted the data well, with coefficients of determination (r^2) of 0.94–0.99 for the four groups. The rate of growth (slopes) did not differ among the four groups (ANCOVA, F=1.40, P=0.25). However, the June laboratory group was significantly larger at a given age than the wild fish (ANCOVA, F=5.05, $P < 0.01$; Tukey pairwise comparison), but the remaining groups did not differ in their length-at-age.

The distribution of spawning dates, based on counts of otolith increments, indicated that spawning occurred from March to July in 1987, and from

Table 1

Mean dry weight in micrograms (μg) and as a percentage of total weight (in parentheses) and frequency of occurrence of prey items in stomachs of white seabass caught along the coast. Six fish with empty stomachs were excluded from the analysis. *n* = sample size.

	Length class and mean length (mm SL)					
Prey category	6–10 (7.9)	10–18 (13.7)	18–25 (21.8)	25–35 (29.1)	35–55 (44.8)	55–150 (79.2)
Mean Dry Weight in μg and (%)						
Mysids	46 (75)	154 (91)	467 (99)	1,417 (99)	2,329 (78)	8,270 (74)
Copepods	10 (16)	2 (1)	—	—	—	—
Gammarid amphipods	—	7 (4)	—	5 (<1)	11 (<1)	—
Fish	—	—	4 (1)	—	97 (3)	768 (7)
Shrimp	—	—	—	—	186 (6)	211 (2)
Nematodes	—	—	—	—	6 (<1)	15 (<1)
Macrophytes	—	—	<1	—	55 (2)	647 (6)
Crustacean parts	5 (8)	2 (1)	—	5 (<1)	—	459 (4)
Sand	—	—	—	1 (<1)	185 (6)	—
Unidentified	—	5 (3)	—	—	99 (3)	814 (7)
Total	61	170	471	1,428	2,968	11,184
Frequency of occurrence (%)						
Mysids	78	91	100	96	100	100
Copepods	11	5	—	—	—	—
Gammarid amphipods	—	5	—	11	5	—
Fish	—	—	5	—	25	25
Shrimp	—	—	—	—	5	5
Nematodes	—	—	—	—	5	10
Macrophytes	—	—	5	—	25	50
Crustacean parts	11	5	—	4	5	15
Sand	—	—	—	4	5	—
Unidentified	—	5	—	—	15	10
n	18	22	20	27	20	20

March to the beginning of September in 1988 (Fig. 10). In both years, most of the young white seabass collected were spawned in June. The distribution of spawning dates derived from estimated ages agreed closely with those based upon direct ageing.

Discussion

Spawning season

Larval and juvenile white seabass collected off San Diego County were spawned from March to September, with the greatest number spawned in June in both years (Fig. 10). This seasonal pattern of spawning, inferred from counts of otolith increments, agrees with previous estimates based on larval abundance and adult spawning condition. Moser et al. (1983) observed that eggs and larvae were most abundant in CalCOFI

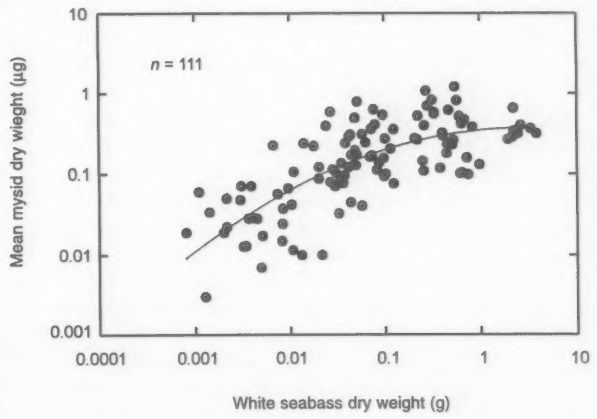

Figure 6

Relation between white seabass dry weight and mean dry weight of mysids (total weight of mysids plus total number of mysids) in the stomachs of 111 white seabass.

plankton samples in July and that 95% of fish were captured between May and August. Adults begin to mature in early March (Clark, 1930) and spawn off southern California from April to August. Peak spawning activity is in May and June (Skogsberg, 1939).

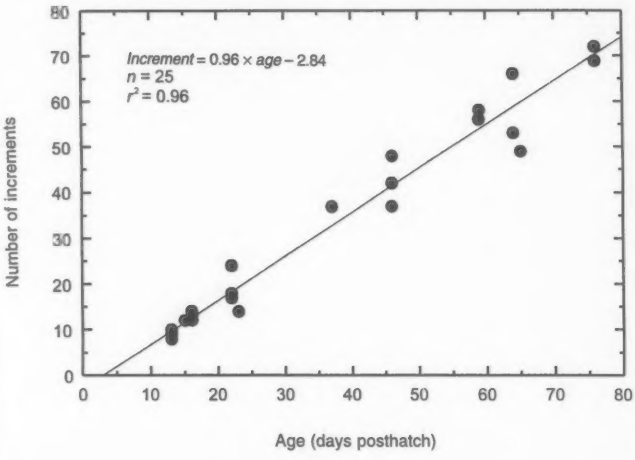

Figure 7

Relation between observed number of increments in a sagitta and known age of 25 laboratory-reared white seabass.

Size and age at settlement

The smallest larvae caught during the present study were 6–7 mm SL, which would seem to indicate that white seabass begin to settle at about this size. However, white seabass as small as 4.2 mm SL were collected along the open coast north of San Diego County in 1988 and 1989 with a trawl containing 2-mm mesh in the codend (Allen and Franklin, 1992); therefore the smallest settled larvae were probably not retained by our net. More than 20% of the individuals collected in that study were <5 mm SL and 50% were <7 mm SL. This size distribution suggests that many larvae caught off San Diego County had settled at lengths of 4–5 mm SL. Larvae up to 7.2 mm SL have been collected from the water column (Moser et al., 1983), indicating that some individuals settle at >5 mm SL.

Given that many white seabass settled at 4–5 mm SL, the average age at settlement must be less than one month. The 10 smallest fish caught and aged in this study ranged from 6.2 to 9.2 mm SL and were 26–32 d old (Fig. 8). Although smaller (4–5 mm SL) fish were not aged, they were probably much younger. In the laboratory, white seabass reared at 15°C hatch at a length of 2.8 mm SL after 2 d and grow to 4 mm SL in 10 d and to 5 mm SL in 15–19 d (Moser et al., 1983; Orhun, 1989). At this rate of growth, a 4–5 mm SL settled fish would have spent only 12–21 d in the pelagic habitat.

Allen and Franklin (1992) hypothesized that most white seabass larvae that settle along the coast of southern California are spawned off Baja California and advected northward. However, a short pelagic phase of 2–3 weeks suggests that many of these larvae are spawned within the Southern California Bight (SCB). The direction of larval transport is difficult to predict because the behavior and position of white seabass larvae in the water column is unknown. During spring and early summer, poleward-flowing undercurrents over the continental slope and equatorward-flowing surface currents over the continental shelf (Hickey, 1993) could transport larvae along the coast in either direction. However, mean seasonal current velocities in the SCB region in spring and early summer are generally less than 20 cm/s, although short-term velocities can be higher (Hickey, 1993). At 20 cm/s, larvae could be transported a maximum of 200–360 km in 12–21 d. It therefore seems unlikely that the 4–5 mm SL white seabass caught in the northern and middle SCB by Allen and Franklin (1992) were spawned off Mexico. These larvae, which represented a large proportion of the total catch, were almost certainly spawned off California. Of course older larvae collected in the middle SCB or young larvae caught off San Diego County could have been spawned off either California or Mexico.

Nursery location

The depth distributions of settled white seabass on the coast and within bays suggests that these fish prefer shallow water beyond the surf zone. Along the open coast, nearly all fish were caught at depths of 4–8 m, a region which begins just beyond the breaking waves. In the bays, all 10 fish were caught just beyond the shore break at a depth of 0–1 m. Previous observations in other regions are consistent with this conclusion. Settled white seabass have been collected beyond the breaking waves along semi-protected and exposed shores in and around Long Beach Harbor (Allen and Franklin, 1988). White seabass were not collected along protected shores, but depths <1.5 m were not sampled. On the open coast north of San Diego County, settled white seabass were also more abundant along the 5-m

depth contour than along the 10-m contour (Allen and Franklin, 1992). Although this distribution supports the conclusion that white seabass prefer shallow water, 30–40% of the settled fish were caught at the 10-m contour (Allen and Franklin, 1992). Most of the fish collected at 10 m were taken along one section of coastline between Ventura and Point Dume; thus the preference for shallow water may be modified by local conditions.

Greater densities of settled fish along the open coast than in the bays suggests that the primary nursery for white seabass is the open coast. However, this difference in densities may reflect lower capture efficiencies of the 1.0-m trawl and beach seine in comparison with the 1.6-m trawl used on the coast. Although net efficiencies could not be estimated for white seabass because of low abundance, Kramer (1990) found no difference in efficiency of these same nets for California halibut <40 mm SL. Net efficiencies probably did not differ greatly for small white seabass either, and thus the low catch of settled fish in the two bays was due to low abundance. In ichthyofaunal surveys of other southern California bays over the last several decades, only a few early juvenile white seabass have been caught (Dixon and Eckmayer, 1975; Klingbeil et al., 1975; Horn and Allen, 1981). Although depths of 0–1 m may not have been sampled intensively, data from these surveys support the view that bays as a whole are not important nurseries for white seabass.

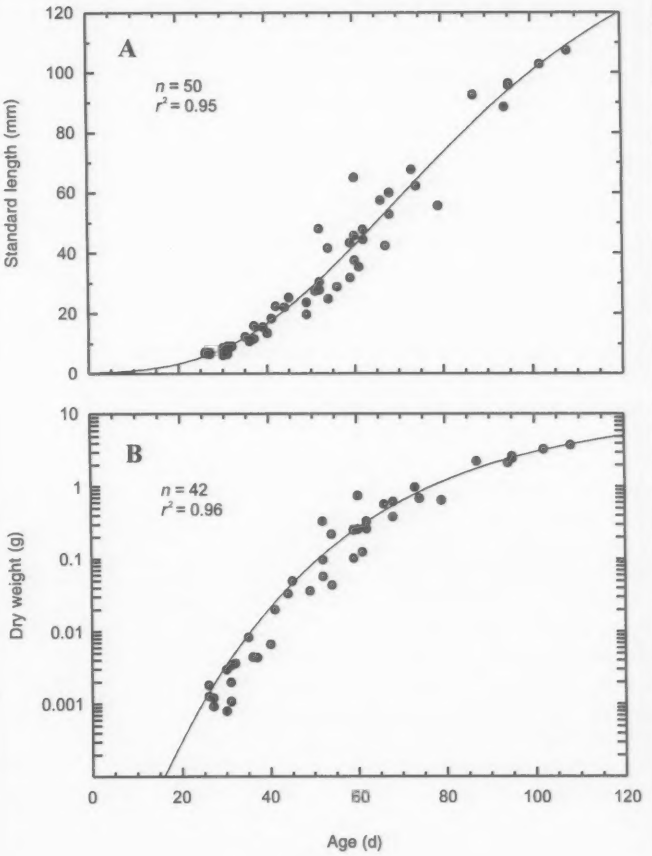

Figure 8

Gompertz growth curves relating (**A**) length and age, and (**B**) weight and age of recently settled white seabass. Ages were determined from counts of increments in sagittae.

The small size of southern California bays must also limit their importance as nursery areas for white seabass. As an example, Kramer (1990) estimated there were only 92 ha of habitat available between 0 and 1 m in Mission Bay and only 10 ha in Agua Hedionda Lagoon, compared with roughly 2,500 ha of habitat available between 5 and 8 m along the coast of San Diego County. Most of the remaining bays on the southern California coast are also small and many are periodically closed off from the sea by shifting sandbars (Zedler, 1982).

Nursery features

The narrow depth distribution of settled white seabass along the coast suggests that one or more features of this zone enhance survival of young fish. Survival in shallow nurseries may be higher because of faster growth resulting from abundant food or warmer water, or lower predation rates (Bergman et al., 1988; Karakiri et al., 1989). Two features of the white seabass nursery that may promote rapid growth of juveniles are the abundant mysids and warmer water. Mysids, the principal prey of all sizes of white seabass collected, appear to be much more abundant within the nursery than at adjacent depths. Clutter (1967) sampled mysids at depths of 2–14 m during 1960–62 at a site 3 km south of the Torrey Pines 2 site (Fig. 1). Although the center of the depth distribution varied among months by 1–2 m, the mysid *Metamysidopsis elongata* was most numerous in the middle of the white seabass nursery

(Fig. 3). Other species of mysids were much less abundant. Density of *M. elongata* within the nursery can be quite high. Clutter's data indicate that the mean density of mysids at 6 m was over 4,000/m^3, whereas Roberts et al. (1982) estimated that the mean density of mysids at 6 m near the San Onofre site was over 100/m^3. Mysids are also about an order of magnitude more abundant during spring and summer, when white seabass are in the nursery (Clutter, 1967).

Mysids are not only abundant within the nursery; their broad size distribution makes them suitable prey for both recently settled larvae and much larger juveniles. Mature *M. elongata* brood and release relatively large young that remain in shallow water (Clutter, 1967). This reproductive strategy results in a population of mysids in the nursery that ranges over 100-fold in individual weight (Fig. 6). Although larger fish eat larger mysids, juveniles >40 mm SL can apparently feed on the largest mysids available (Fig. 6). At about this size, a transition from mysids to larger prey such as fish and shrimp also begins. The diets of other closely related sciaenids show a similar shift. Small (10–40 mm SL) sand seatrout, *Cynoscion arenarius*, small (15–30 mm SL) spotted seatrout, *C. nebulosus*, and juvenile (50–129 mm SL) weakfish, *C. regalis*, all feed extensively on mysids and at larger sizes shift to eating fish (Stickney et al., 1975; Sheridan, 1979; McMichael and Peters, 1989). Large juvenile, subadult, and adult white seabass feed principally on fish (Quast, 1968; Thomas, 1968).

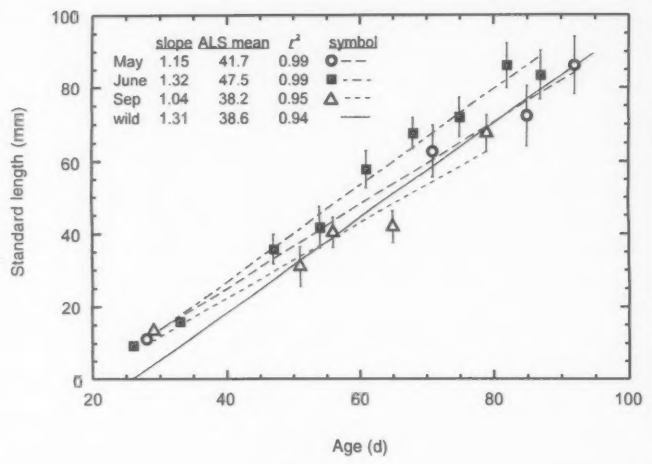

Figure 9

Estimated linear growth rates of wild white seabass (n=50) and three groups of juveniles spawned on 8 May, 24 June, and 25 September 1989 and reared at 17–20°C. Symbols represent the mean length (± 1 SD) of a subsample of 16–76 reared fish. For clarity, symbols are not shown for wild fish. Slopes, adjusted least squares (ALS) means, and coefficients of determination (r^2) are shown.

A second feature of the shallow nursery that may enhance growth and survival of settled white seabass is warm water. Temperatures in the 4–8 m stratum during the summer ranged from 16 to 20°C, an average of 1.2 and 1.8°C warmer than the two deeper strata. The effect of a 1–2°C increase on growth has not been calculated for juveniles, but Orhun (1989) observed that a temperature increase from 15 to 17°C resulted in an increase in growth rate (dry weight gain) from 13.8%/d to 16.7%/d in 4–21 d old larvae. Temperature may have less influence on growth of juveniles, but any increase in growth rate will accumulate over the 2–3 months that juveniles are in the shallow nursery. Houde (1987) has demonstated that a small increase in growth rate acting over a moderate time interval can reduce stage duration and theoretically result in substantial increases in survival and cohort size.

Correlations between abundances of drift macrophytes and white seabass suggest that macrophytes are also an important feature of the nursery. Although the correlation among abundances in single tows was weak (r=0.29), the sensitivity of this analysis was poor because the catch of white seabass was low; a maximum of only two white seabass was caught in a single tow at these stations. The correlation among mean abundances in the four tows at each site—the mathematical equivalent of making longer tows—was stronger (r=0.52) and does suggest that white seabass are more common near drift macrophytes. Allen and Franklin (1992) also noted that white seabass were rarely caught unless drift algae was present. It is possible that white seabass are simply more vulnerable to the trawl when drift macrophytes are present, but numerous studies with drop nets and purse seines have demonstrated that many juvenile fishes associate with drift macrophytes (Kulczycki et al., 1981; Robertson and Lenanton, 1984; Kingsford and Choat, 1986). Small white seabass may associate with drift macrophytes because they harbor suitable prey or serve as a refuge from predation.

In addition, the nursery area may be preferred by white seabass because the risk of predation could be lower than at adjacent depths. Unfortunately this hypothesis is difficult to evaluate. Surveys of the nearshore areas of southern California show that

predators of small benthic fishes are present both within the white seabass nursery and in deeper water (Love et al., 1986). Some of these predators, such as the California lizardfish (*Synodus lucioceps*), are less abundant within the white seabass nursery than at 12–18 m, whereas other species, such as California halibut (*Paralichthys californicus*), are more abundant within the nursery than in deeper water (Ford, 1965; Love et al., 1986; Allen, 1990). However predation risk will depend not only on the total number of vertebrate and invertebrate predators at a particular depth, but also on the size and ontogenetic distribution of predators as well as species-specific probabilities of encounter, detection, and capture (Bailey and Houde, 1989; Fuiman and Margurran, 1994). A detailed study is required to determine if the risk of predation to settled white seabass is lower in the nursery than in deeper waters.

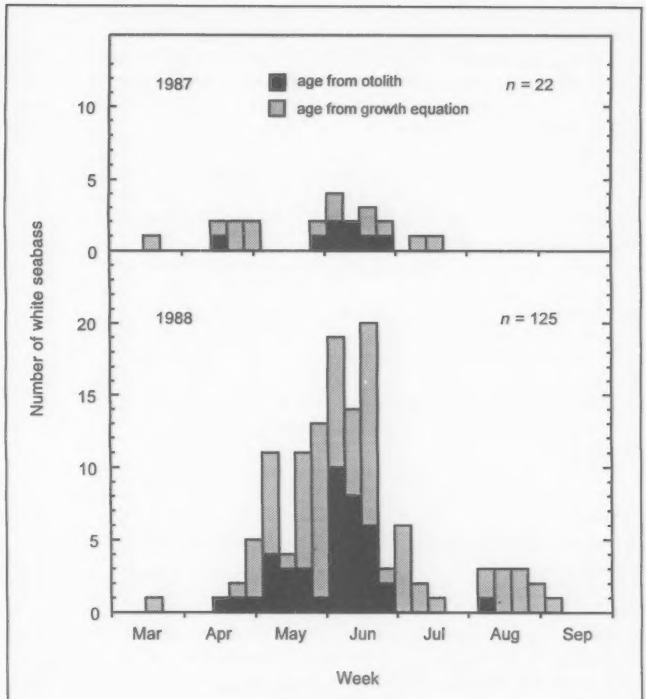

Figure 10

Seasonal pattern of spawning by white seabass in 1987 and 1988 as calculated from date of capture, age of settled fish, and an estimated two-day incubation period (Orhun, 1989). The ages of 50 fish were estimated directly from otoliths, the others from the age-length relation shown in Figure 8.

Conclusion

The shallow water along the open coast just beyond the breaking waves appears to be the primary nursery for white seabass. Survival of young white seabass is probably influenced by the abundance of mysids and drifting macrophytes as well as by water temperature in the nursery during spring and summer. However, it is not known if survival in the nursery is an important determinant of year-class success for white seabass. Year-class success in most marine fishes is generally believed to be set during the larval stage. However, poor correlations between larval abundance and subsequent recruitment for some species indicate that survival of older fish, perhaps early juveniles, may be equally important (Sissenwine, 1984; Bradford, 1992). Further studies are needed to evaluate the importance of survival of early life history stages in determining the distribution and abundance of white seabass populations off southern California.

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Analysis of diet and feeding strategies within an assemblage of estuarine larval fish and an objective assessment of dietary niche overlap

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Abstract.—Fish larvae and zooplankton were sampled during seven consecutive months from four regions of Wilson Inlet, an estuary in southwestern Australia. Mouth size, prey size, and dietary composition of larvae of the gobiids *Afurcagobius suppositus*, *Pseudogobius olorum*, and *Favonigobius lateralis*, the blenniid *Parablennius tasmanianus*, and the syngnathid *Urocampus carinirostris* were determined. Dietary niche overlap (DNO) was calculated for co-occurring species pairs, both with and without incorporating a measure of relative prey (zooplankton) abundance. Significance of DNO was assessed 1) objectively, with bootstrapping of the dietary data and 2) subjectively, by assigning significance to values >0.6. The diet of *A. suppositus* was dominated by harpacticoids, polychaete larvae, and the calanoid *Gladioferens imparipes*, whereas diets of the other species were dominated by copepod nauplii and postnaupliar stages of the cyclopoid *Oithona simplex*, the proportions of the latter increasing with growth of the larvae. Small numbers of large and small prey items were found in the stomachs of *A. suppositus* (mean=2.5), which had the largest mouth, whereas large numbers (mean=28.7) of small prey and no large items were found in the stomachs of *P. tasmanianus*, which had the second largest mouth. Between these extremes, *P. olorum*, *U. carinirostris*, and *F. lateralis* each ate mostly small and intermediate-size prey, supplemented by a few large prey. The data did not support the hypothesis that an increase in the difference in gape size between species would decrease the prevalence of significant DNO. The lack of a consistent relation between mouth size and DNO among the five species is evidence that interspecific dietary differences reflect differences in feeding behavior. With bootstrapping, the prevalence of significant ($P<0.05$) DNO between species pairs was 32.6% when prey data were included in the analyses and 46.5% when prey data were not included. By subjectively assigning significance to DNO values >0.6, we obtained substantially less conservative estimates that indicated the prevalence of significant DNO was >53%.

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Starvation has been considered a major cause of mortality in larval fish (e.g. Hunter, 1984), although evidence from the field has been difficult to obtain (Heath, 1992). If starvation occurs within an assemblage of larval fish, competition for food is expected to contribute to that starvation. However, indications of any such competition may go undetected if the diet of only a single species is examined or if the influence of other planktivores (Fortier and Harris, 1989) is not considered. In the case of larval fish, relatively few studies have examined in detail the diets of several co-occurring species (e.g. Last, 1980; Laroche, 1982; Govoni et al., 1983; Watson and Davis, 1989). Furthermore, no study has objectively assessed the significance of dietary niche overlap (DNO), where DNO refers to the amount of sharing of food resources among larval fish. Assessments of whether dietary overlap within or between species (including larval fish) is significant have been based on indices that range from 0 for no overlap to 1 for complete overlap, with values greater than 0.5, 0.6, or 0.7 considered to be significant (e.g. Harmelin-Vivien et al., 1989; Cervellini et al., 1993; Vega-Cendejas et al., 1994; Hartman and Brandt, 1995). However, because these cutoff points are arbitrary, they are not necessarily biologically significant, as in the case with fish larvae where individuals of co-occurring species may be confronted with large concentrations of the same prey type and thus any similarities in diet may be due to chance encounters.

Although dietary compositions of larval fish have been considered in the context of the abundance of the zooplankton prey of those larvae (e.g. Dagg et al., 1984; Jenkins, 1987; Hirst and DeVries, 1994; Welker et al., 1994), no study of dietary overlap between larval fish has incorporated data on their zooplankton prey. This analysis is necessary in order to assess whether there is a likelihood of competition for food.

Differences in mouth structure of fish may lead to differences in feeding success on particular prey types (Lavin and McPhail, 1986). Co-occurring larvae of different species with similar-size mouths may therefore exhibit a higher rate of significant DNO than those with mouths of different size. Because fish larvae usually swallow prey

whole, mouth size limits prey size; thus prey width is typically the limiting dimension for ingestion (e.g. Hunter, 1984, Heath, 1992). It is therefore important to examine mouth size and prey width when exploring the trophic relations of larval fish.

The first aim of this study was to examine the relation between mouth width, prey width, and dietary composition of the larvae of five teleosts in an estuary. The dietary data were then used to examine the extent of DNO between these species with a technique that takes into account relative prey concentrations. With this procedure we were able to test the hypothesis that divergence in gape size between species should be accompanied by a decrease in the prevalence of significant DNO between these species. Bootstrapping was used to assess whether species-pair DNO values were significant. The results of using this robust approach were compared with those obtained when relative prey concentrations were not included in the calculation of DNO and when a subjective level of >0.6 was considered to be significant for the DNO values.

Materials and methods

Sampling methods

This study was carried out in Wilson Inlet (35°00'S, 117°24'E), an estuary in southwestern Australia that comprises a 48 km^2 basin with two main tributaries, the Denmark and Hay rivers. Although samples were collected monthly between July 1988 and June 1989, the data used in this paper are restricted to those obtained between October 1988 and April 1989 when fish larvae were most abundant. Ichthyoplankton and zooplankton were sampled from open waters of the upper, middle, and lower basin, and the central channel of the lower saline reaches of the Denmark River, located 10.7, 8.3, 2.0, and 7.3 km, respectively, from the estuary mouth. The water depth in each region was between 2 and 3 m.

Sampling was initiated soon after sunset to reduce the likelihood of larvae avoiding the plankton nets. Fish larvae were collected with a pair of 500-µm-mesh conical nets, each with a mouth diameter of 0.6 m and a length of 2 m. The nets were attached to either side of a powerboat and towed for 10 min just below the surface of the water at a speed of 1.5 m/s. During each ichthyoplankton tow, three to five zooplankton samples were taken from the surface with a conical, 53-µm-mesh net with a mouth diameter of 0.35 m. The volumes of water filtered during each ichthyoplankton and zooplankton tow were measured with flowmeters. The zooplankton tows were 7–10 s in duration. The flowmeter in the zooplankton net was closely observed during each tow. A tow was immediately terminated if the propeller speed suddenly decreased—a sign that the net was clogging. Samples were fixed in a 5% solution of formalin, which was replaced with 70% ethanol on the following day. The detailed results of the zooplankton sampling are given in Gaughan and Potter (1995).

Laboratory procedures and data analyses

Zooplankton were identified and counted under a dissecting microscope from subsamples of the replicate samples. Counts were standardized to numbers/m^3; thus mean concentrations of taxa at each region within each month were able to be calculated. Relative proportions of those zooplankton taxa that contributed to larval diets at any time during the study were calculated for each sample. These represented relative resource availability (R_i).

The gobiids *Pseudogobius olorum*, *Afurcagobius suppositus*, and *Favonigobius lateralis*, the blenniid *Parablennius tasmanianus*, and the syngnathid *Urocampus carinirostris* were chosen for the present study because their larvae are abundant in Wilson Inlet from late spring to early autumn (Neira and Potter, 1992), collectively contributing 70.8% of the total open-water assemblage of larval fish in this estuary between September 1987 and April 1989.

All larvae of each species in a sample were removed and counted. Body length (BL) of each larva (i.e. the distance from the snout to tip of notochord in preflexion and flexion larvae and from the snout to the posterior end of the hypural plate in postflexion larvae [Leis and Trnski, 1989]) was measured to the nearest 0.1 mm. Since a focus of this study was the comparison of mouth width with prey width, the diets of individual size classes of larvae were determined. However, because the analyses of DNO were undertaken for co-occurring species within individual samples, the dietary data for all size classes of each species were pooled (see below).

The smaller larvae of *P. olorum*, *P. tasmanianus*, *F. lateralis*, and *A. suppositus* were each grouped into 1.0-mm length classes. Because *P. olorum* and *P. tasmanianus* >5 mm BL and *F. lateralis* and *A. suppositus* >6 mm BL were rarely caught, larvae of these four species longer than these respective lengths were each grouped into single length classes. Because the length range of *U. carinirostris* was relatively wide, the larvae of this species were grouped into length classes with intervals of 3 or 4 mm, depending on the numbers caught.

Items in the gut were identified and counted. Maximum widths of intact dietary items, which typically

represent the limiting dimension for ingestion, were measured to 0.01 mm with an ocular micrometer in a compound microscope. Mouth width of larvae at the widest point of the upper jaw was similarly measured on a subsample of at least 50 larvae of each species. Widths of prey and mouth widths of larvae of each species were then plotted against body length of larvae.

Proportional utilization (p_i) of each prey type was calculated for length classes within each species with data pooled across regions and months. Proportional utilization was also calculated across length classes for the larvae of each species within a sample. Guts that were empty or contained only unidentifiable material were not included in these calculations.

Relative feeding prevalence of all larvae within samples were correlated against the corresponding estimates of zooplankton abundance to determine if there was any evidence that zooplankton abundance was limiting feeding success. The average DNO exhibited between all species within samples was likewise compared with zooplankton abundance.

Calculation of dietary niche overlap

Interspecific DNO was calculated for species-pairs within individual samples, i.e. for each site within a given month. Because this part of our study focused on examining niche relations between species, pooled diets for each species within a sample were considered to represent the average diet of each species. Furthermore, comparisons were limited to those samples in which ≥10 larvae of each of two or more species contained food. By pooling data across size classes we were able to compare more DNO data. Although the use of average diets would reduce the robustness of a parametric test of significance, we used nonparametric techniques for assessing the significance of DNO.

Sufficient numbers of larvae were obtained for analysis in 13 of the 28 ichthyoplankton samples (7 months × 4 regions) to allow 43 pairwise comparisons to be made between the diets of co-occurring species.

Besides the DNO values that were calculated and that incorporated prey abundance data, the results of this technique were also evaluated against calculations of DNO that did not incorporate such data. Because prey abundance data are incorporated into prey utilization data prior to calculating DNO (see below), the same formula was used to calculate DNO both with and without consideration of prey concentrations. DNO was measured with the symmetric niche overlap coefficient (Pianka, 1973)

$$\Phi_{ij} = \left(\sum p_{ij} p_{ik}\right) / \sqrt{\left(\sum p_{ij}^2 \sum p_{ik}^2\right)},$$

where p_{ij} and p_{ik} = the proportional utilization of prey type i by species j and k, respectively.

Using the p_i data directly, we were able to provide a basis for calculating DNO without prey abundance data. To incorporate prey abundance data, the geometric mean (g_i) of p_i and electivity (e_i) was used (Winemiller and Pianka, 1990), instead of p_i as in the original formula. The geometric mean gives a better indication of ecological similarity by reducing those biases within both p_i and e_i that can result from the presence of very abundant or very rare prey types (Winemiller and Pianka, 1990). Electivity is the p_i value that has been weighted by resource availability (R_i) as $e_i = p_i/R_i$. These values were calculated within the DNO algorithm and are not presented. Note that g_i can be used with other overlap indices because it is calculated prior to the calculation of the overlap value.

Bootstrapping of the resource matrix of a pair of species was used to obtain a null distribution of 1,000 pseudo-DNO values against which the significance of observed DNO could be assessed (Winemiller and Pianka, 1990). These calculations were performed for species pairs at sites within months. In each one of the 1,000 runs, the algorithm randomly reassigned the g_i values for each prey type (e.g. resource states $i...p$) within each larval species j and k, but among the resource types used by both j and k (e.g. amongst $g_{ij}...g_{nj}$ and $g_{ik}...g_{pk}$). A g_i value for one of the species pair may thus be reassigned to a resource state which was used only by the other species.

The null hypothesis (H_0) for each test was that the dietary compositions of the larvae of the two species were not the same. The null hypothesis was rejected if more than 95% of the 1,000 pseudo-DNO values were less that the observed DNO. Such cases indicated that the observed value was larger than would be randomly expected at $P<0.05$.

The prevalence of significant DNO calculated with g_i and bootstrapping was then compared with that obtained with p_i, i.e. when R_i was not taken into account. These results were also compared with those obtained when the significance of DNO was arbitrarily set at values >0.6.

Results

Zooplankton

Zooplankton were very abundant in Wilson Inlet between October 1988 and April 1989; there was a total mean monthly concentration of 342,746 organisms/m^3 (range = 48,641–2,951,209/m^3). Concentrations exceeded 100,000/m^3 in 26 of the 28 zooplank-

ton samples. Mean monthly concentrations of zooplankton in Wilson Inlet were similar from October 1988 to April 1989; only January had a significantly ($P<0.05$) higher concentration (Gaughan and Potter, 1995).

All copepods, irrespective of stage, contributed 74.7% of the total mean concentration of zooplankton (Table 1). The cyclopoid *Oithona simplex*, the calanoids *Gladioferens imparipes* and *Acartia simplex*, and several species of harpacticoids were the only copepods that were common in Wilson Inlet (Gaughan and Potter, 1995). Considering just the copepods, adults of *A. simplex* and *G. imparipes*, which represented the largest prey types consumed by fish larvae in Wilson Inlet, contributed only 2.9% of the total mean concentration of this taxonomic group. The smaller species and developmental stages of copepods were thus approximately 33 times more abundant than the adults of *A. simplex* and *G. imparipes* collectively. The mean concentrations and relative contributions of other zooplankton taxa that were eaten by larval fish during this study are shown in Table 1.

Numbers of prey items consumed and dietary composition of fish larvae

The total number of larvae of each species examined during this study are shown in Table 2, and the numbers of larvae in size classes of each species which contained food are shown in Figure 1.

The mean number of prey items found in each larva was less than five for *A. suppositus* and *F. lateralis*, between five and ten for *P. olorum* and *U. carinirostris* and 28.7 for *P. tasmanianus* (Table 2). Likewise, the maximum numbers of prey consumed were much lower for the first four species than for *P. tasmanianus* (Table 2). The number of prey ingested by larvae increased with body size only in the case of *U. carinirostris*.

Various developmental stages of copepods dominated the diets of larval fish in Wilson Inlet; the rotifer *Synchaeta* cf. *baltica* and the larvae of bivalves and polychaetes were also occasionally important (Fig. 1). Only the postnaupliar stages of copepods in the diets were identified to species. Each of the common types of copepod contributed to the diets of fish larvae.

During the growth of *P. olorum*, *F. lateralis*, *U. carinirostris*, and *P. tasmanianus*, the contribution of copepod nauplii declined while that of postnaupliar stages increased (Fig. 1). *Oithona simplex* was particularly important to *P. olorum* and *U. carinirostris*, representing over 30% of the diet of the three largest size classes of the former species and over 40% of the diet of all size classes of the latter species. By contrast, despite the increased contribution by *O. simplex* to larger size classes of *P. tasmanianus*, copepod nauplii dominated the diet of all size classes, contributing > 40% to each (Fig. 1). The diet of *F. lateralis* <4.0 mm BL consisted mainly of copepod nauplii and to a lesser extent of bivalve larvae and *O. simplex*. The main prey types of *F. lateralis* from 6.0–7.9 mm BL were harpacticoids (40.9%), calanoid copepodites (20.6%), and phytoplankton (15.6%).

Polychaete larvae, copepod nauplii, and harpacticoids each contributed over 25.0% of the diets of the smallest size class of *A. suppositus*, whereas harpacticoids alone contributed 60.0% to larvae >6.0 mm BL (Fig. 1). Harpacticoids also contributed 15.3 and 27.0% of the diet in the 4.0–4.9 and 5.0–5.9 mm length classes, respectively. *Gladioferens imparipes*

Table 1

Mean monthly concentrations and relative contributions of zooplankton in Wilson Inlet between October 1988 and April 1989.

Taxa	Mean concentration (no. organisms/m^3)	Relative contribution (%)
Copepod nauplii	164,827	48.1
Calanoid copepodites	33,755	9.8
Oithona simplex	44,629	13.0
Acartia simplex	6,771	2.0
Gladioferens imparipes	719	0.2
Harpacticoids	5,523	1.6
Polychaete larvae	34,997	10.2
Bivalve larvae	18,435	5.4
Synchaeta cf. *baltica*	9,787	2.9
Other taxa	23,303	6.8
Total	342,746	

Table 2

Mean and maximum numbers of prey per larva for five teleost species in Wilson inlet. n = the total number of larvae of each species examined.

Species	n	Mean prey/larva	Maximum prey/larva
Pseudogobius olorum	1,946	7.7	30
Favonigobius lateralis	451	4.0	15
Afurcagobius suppositus	485	2.5	19
Parablennius tasmanianus	469	28.7	103
Urocampus carinirostris	434	9.7	23

was abundant only in the diet of the 4.0–4.9 and 5.0–5.9 mm length classes (Fig. 1).

Prey width and larval mouth width

Urocampus carinirostris had the smallest mouth, *P. tasmanianus* and *A. suppositus* the widest mouths (Fig. 2, A, D, E). The shapes of the mouths were most similar in the case of *P. olorum* and *F. lateralis* (Fig. 2, B and C). Although mouth width of *U. carinirostris* increased linearly with body length (Fig. 2A), such an increase in the other four species was best described by a polynomial function (Fig. 2, B–E: Table 3). Mouth width of *U. carinirostris* increased slowly from 0.19 mm at 8 mm BL to 0.28 mm at 19 mm BL (Fig. 2A). The rate at which mouth width increased with body length was greater for the other four species (Fig. 2, B–E). In *A. suppositus*, mouth width increased from 0.33 mm at 3.5 mm BL to 0.68 mm at 6.0 mm BL (Fig. 2E). The smallest larvae of *P. olorum*, *F. lateralis*, and *P. tasmanianus* had narrower mouths (<0.15 mm) than both *A. suppositus* and *U. carinirostris*, owing to their smaller size upon arrival in the plankton (Fig. 2, A–E). However, mouth widths of the first three of these species exceeded the maximum recorded for *U. carinirostris* (0.28 mm) by the time each had attained 5 mm BL and approached 0.60 mm in larger larvae.

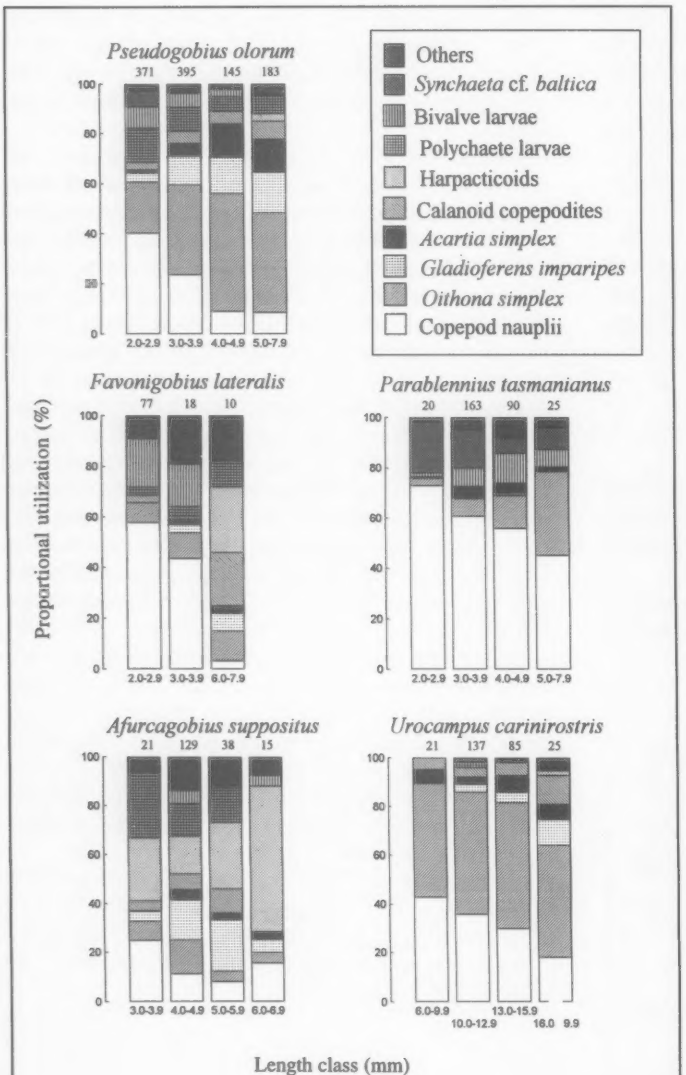

Figure 1

Proportional utilization (p_i, %) for length classes of larvae of five species of fish caught at four sites in Wilson Inlet between October 1988 and April 1989. The numbers of larvae that contained food in each size class are shown above the bars.

The slope describing the relation between prey width and larval length for each species was less than 0.03. The extent to which prey width increased with length was thus very small for each species. Minimum prey width for each species was about 0.04 mm (Fig. 2, A–E). The large numbers of prey of each species with widths of 0.04–0.08 mm were predominantly attributable to copepod nauplii. Prey widths of between 0.04 and 0.18 mm predominated in *U. carinirostris*, *P. olorum*, and *F. lateralis* (Fig. 2, A–C).

Parablennius tasmanianus ate mainly prey 0.04–0.13 mm wide, but with a maximum width of only 0.18 mm (Fig. 2D). *Afurcagobius suppositus* consumed the largest prey items, i.e. postnaupliar stages of *G. imparipes* and *A. simplex*, with widths of 0.12–0.30 mm and 0.10–0.16 mm respectively. As with the other species, *A. suppositus* also ate smaller items (0.04–0.10 mm) (Fig. 2E).

As *U. carinirostris*, *P. olorum*, *F. lateralis*, and *P. tasmanianus* grew, they continued to eat many prey <0.10 mm wide, even though the smaller larvae of each were capable of eating prey >0.10 mm (Fig. 2, A–D). Prey width was about 0.10 mm narrower than mouth width for most of the length range of *U. carinirostris* (Fig. 2A). The widths of the larger

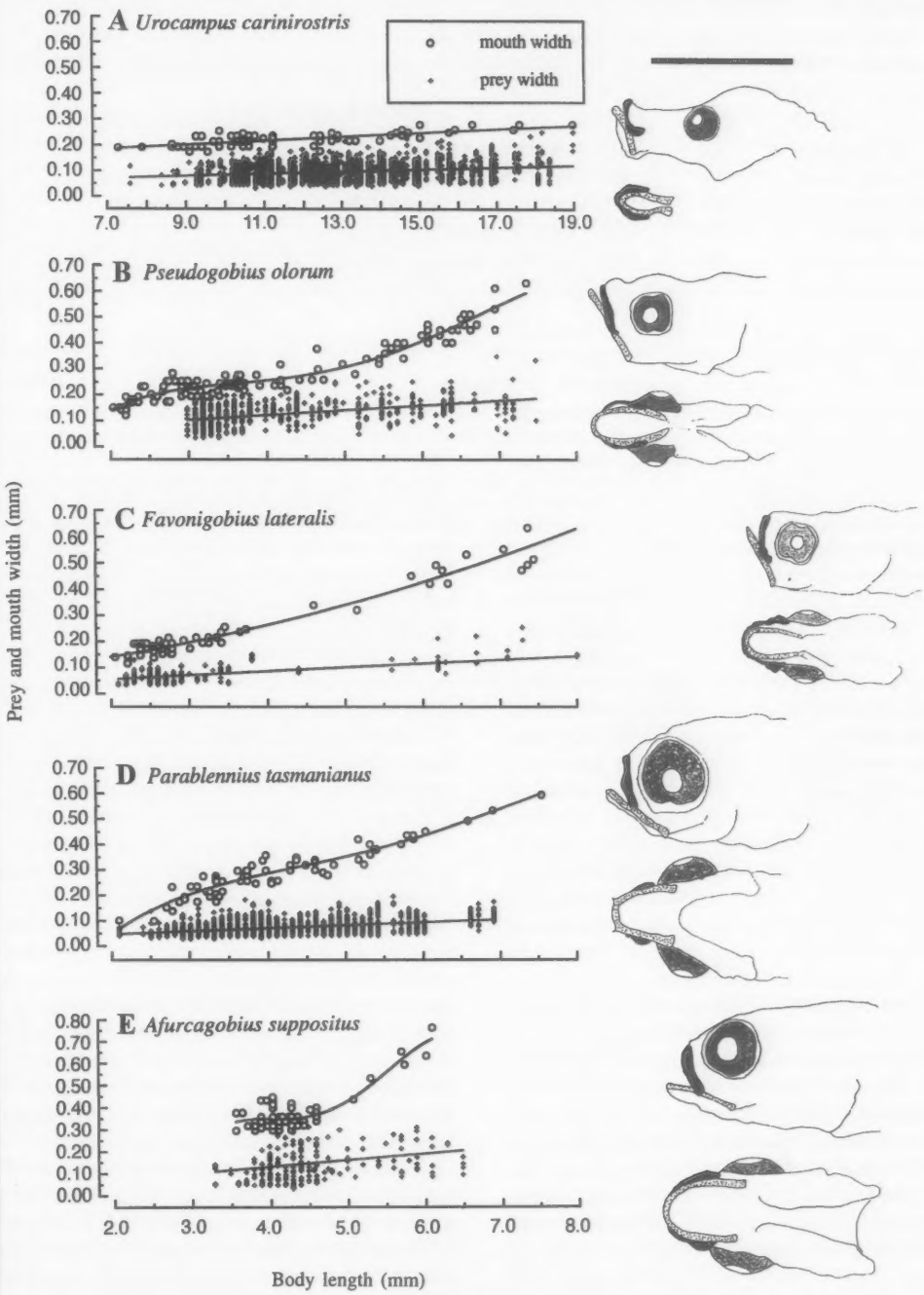

Figure 2

Prey width and larval mouth width for larvae of five species of fish caught in Wilson Inlet between October 1988 and April 1989. Lateral and ventral views of the head of a representative larva of each species are also given; the upper jaw is indicated in black, the lower jaw is indicated with stippling (scale bar equals 1.0 mm). The examples were each taken from a 5.0-mm-BL larva, except the example of *Urocampus carinirostris*, which was taken from a 10.5-mm-BL larva.

Table 3

The relations between mouth width (MW) and body length (BL) for the larvae of five teleost species in Wilson Inlet.

Species	n	Regression function	r^2
Urocampus carinirostris	69	$MW = 0.139 + 0.006(BL)$	0.453
Afurcagobius suppositus	50	$MW = -15.666 + 14.256(BL) - 4.687(BL^2) + 0.671(BL^3) - 0.035(BL^4)$	0.849
Pseudogobius olorum	98	$MW = -0.729 + 0.839(BL) - 0.273(BL^2) + 0.038(BL^3) - 0.002(BL^4)$	0.921
Favonigobius lateralis	50	$MW = 0.061 + 0.029(BL) + 0.005(BL^2)$	0.963
Parablennius tasmanianus	66	$MW = -0.517 + 0.411(BL) - 0.073(BL^2) + 0.005(BL^3)$	0.889

Table 4

The number of cases of significant dietary niche overlap (DNO) for larvae of five teleost species in Wilson Inlet between October 1988 and April 1989. Co-occurring species were compared only when ≥10 individuals of each contained food in their guts. The number of cases for which pairwise comparisons could be made is shown as n. The number of significant cases are presented for DNO calculations I) that used zooplankton concentrations and II) that did not use zooplankton concentrations. Within these categories, the number of significant cases were determined a) at $P<0.05$ from a null distribution derived from bootstrapping and b) with an arbitrary cutoff level for significance at an overlap value >0.6. DNO was measured with a modification of Pianka's (1973) symmetric niche overlap coefficient.

	Pseudogobius olorum n (I) (II) (a, b) (a, b)	*Afurcagobius suppositus* n (I) (II) (a, b) (a, b)	*Favonigobius lateralis* n (I) (II) (a, b)(a, b)	*Parablennius tasmanianus* n (I) (II) (a, b) (a, b)
Afurcagobius suppositus	5 (0, 2) (0, 0)	—		
Favonigobius lateralis	4 (1, 2) (1, 2)	1 (0, 0) (0, 0)	—	
Parablennius tasmanianus	8 (1, 4) (3, 6)	1 (0, 0) (0, 0)	4 (2, 4) (3, 4)	—
Urocampus carinirostris	8 (7, 7) (8, 8)	2 (1, 1) (0, 1)	4 (1, 2) (2, 3)	6 (1, 4) (2, 4)
Totals	n (I) (II) (a, b) (a, b) 43 (14, 23) (20, 28)			
Percent of total	(32.6, 53.5) (46.5, 65.1)			

prey items consumed by *P. olorum* <4.0 mm BL were similar to mouth width, as was also the case with *F. lateralis* of 2.0–2.5 mm BL and *A. suppositus* of 4.0–4.5 mm BL. For each of these three gobiid species, the maximum prey width of larvae >5 mm BL was far less than mouth width. This difference exceeded 0.20 mm in the larger gobiid larvae. Likewise, maximum prey widths for larval *P. tasmanianus* approached mouth width in smaller larvae but were much less for larger larvae (Fig. 2D).

Dietary niche overlap

Dietary niche overlap between *P. olorum* and *U. carinirostris* ranged from 0.543 to 0.983 and was significant on seven of the eight occasions in which these species co-occurred (Table 4). Although DNO ranged from 0.764 to 0.980 on the four occasions that *P. tasmanianus* and *F. lateralis* co-occurred, overlap was significant only twice (Table 4). There were a few other cases of significant DNO amongst the larval fish assemblage; DNO was particularly low between *A. suppositus* and the other species, being significant only with *U. carinirostris* on one occasion.

Of the 43 pairwise comparisons that could be made between the diets of co-occurring larvae of the five species, there were 14 cases (32.6%) of significant DNO (Table 4). This increased to 20 (46.5%) if zooplankton data were not included in the calculations of DNO's. If DNO >0.6 had been considered significant, the number of significant cases increased from 32.6% to 53.5% for calculations which included zooplankton data and from 46.5% to 65.1% for those which did not include these data.

The magnitudes of the differences for the prevalence of significant DNO found by using bootstrap-

ping (18.6% and 20.9%) were greater than those obtained by accounting for zooplankton abundance data (11.6% and 13.9%, Table 4).

Relation between zooplankton abundance and both feeding prevalence and mean DNO

Zooplankton abundance at sites within months was not significantly related to either feeding prevalence ($P>0.05$, $r=0.346$, $n=26$) or mean DNO ($P>0.1$, $r=0.146$, $n=15$) of fish larvae within the corresponding samples.

Discussion

Numbers of prey consumed and prey size

Afurcagobius suppositus, because it ingested larger prey types, e.g. *G. imparipes*, consumed the least number of prey. The other species ate larger numbers of small and intermediate-size prey, e.g. copepod nauplii and *O. simplex*. The significant increase in numbers of prey with length for *U. carinirostris* only was probably attributable to the fact that the magnitude of the range of length of individuals examined for this species was 12 mm, whereas that of the other species was less than 6 mm.

Despite marked increases in mouth width during the growth of each species except *U. carinirostris*, average prey width of the five species increased only slightly with growth. Although smaller larvae consumed prey almost as wide as their mouths, larger larvae typically ate prey far smaller than their mouth size. Furthermore, the smaller larvae of each species consumed some prey items almost as wide as those eaten by larvae in the larger size classes. These data indicate that mouth width was not limiting the ingestion of larger prey types among larvae in the larger size classes.

The dominance of relatively small prey in the diets of larval fish in Wilson Inlet reflects the dominance of these types of zooplankton in the environment. During the study period, copepod nauplii, *O. simplex*, calanoid copepodites and harpacticoids were 33 times more abundant than the adults of *G. imparipes* and *A. simplex* collectively, the only common large prey. Thus, as has previously been found for other larval fish (e.g. Ware and Lambert, 1985; Kellermann, 1990), prey availability strongly influenced the sizes of prey consumed.

From an early age and size, *Afurcagobius suppositus* ate larger prey than the other four species. Since this species hatches at a more advanced stage and with better developed fins than the other four species (Neira et al., in press), they were probably superior swimmers and thus more efficient at capturing larger prey. Greater mobility may have also resulted in *A. suppositus* searching a larger volume of water (Hunter, 1984), which would increase the rate at which the larger and less abundant zooplankton were encountered. The possession of a larger mouth apparently allows *A. suppositus* to take advantage of larger prey in presumably more frequent encounters.

Mouth size and DNO

Although *A. suppositus* had the largest mouth and consumed the largest and most diverse prey, the relative differences in mouth size of the other four species were not accompanied by corresponding differences in the size and composition of prey. A lack of a predictive relation between mouth size and diet has previously been recorded for fish larvae from another estuary (Laroche, 1982) and more recently for larvae of freshwater fish in an experimental situation (Bremigan and Stein, 1994). In Wilson Inlet, this situation was further highlighted by the lack of a relation between the prevalence of significant DNO and the mouth structure of the five species. Thus, the prevalence of significant DNO was not particularly high between *P. olorum* and *F. lateralis* (Table 4), the species with the most similar mouth structure, whereas *P. olorum* and *U. carinirostris* had very similar diets, as indicated by the high prevalence of significant DNO (Table 4), but had different-size mouths. Conversely, the diet of *A. suppositus* overlapped significantly only with that of *U. carinirostris*, the species with the smallest mouth. *Parablennius tasmanianus* and *F. lateralis*, the only other species-pair to exhibit more than one case of significant DNO, also had dissimilar mouths. Finally, *A. suppositus* and *P. tasmanianus* had the largest mouths but the most divergent diets.

Along with the general lack of a relation between mouth size and diet, the relatively frequent occurrence (32.6%) of significant DNO amongst the larval fish in Wilson Inlet, when prey abundance was taken into account,was also attributable to the high concentrations of relatively limited choices of acceptable prey types. The lack of a relation between concentrations of zooplankton and both feeding prevalence and mean DNO within samples was also probably a result of consistently high concentrations of zooplankton. Consequently, significant DNO among larval fish in Wilson Inlet provided no evidence of competition for food. Furthermore, Gaughan and Potter (1995) found that abundances of zooplankton and larval fish were significantly correlated at only two of the four sampling regions in Wilson Inlet. The lack of a rela-

tion at the other two regions was due to large fluctuations in the abundance of zooplankton between months. These fluctuations did not appear to influence monthly trends in the abundance of fish larvae, probably because concentrations of zooplankton typically remained high(>100,000/m^3).

Because in this study we were limited to examining the diets of larval fish, a complete assessment of dietary relations and the potential for competition within the plankton community could not be undertaken. However, other zooplankton taxa (e.g. *Sagitta minima*) sufficiently large to have used the same food resources as larval fish were rare in Wilson Inlet, contributing less than 0.2% of the total numbers of zooplankton (Gaughan and Potter, 1995).

Feeding strategies

The diets of the fish larvae from Wilson Inlet may be viewed as representing a spectrum of feeding strategies.The diet of *A. suppositus* is distinguished from those of the other four species by its broader composition, the larger size of its prey items, and the smaller numbers of prey consumed. At the opposing end of the spectrum, *P. tasmanianus* larvae consumed large numbers of small prey items. The feeding strategies of the larvae of *P. olorum*, *F. lateralis*, and *U. carinirostris* lay between these extremes; these species consumed many small and intermediate-size prey which were occasionally supplemented with larger prey items.

Because the trophic character of a species may be influenced by both size and structure as well as behavior (Lavin and McPhail, 1986), the small influence of mouth width on the size of prey consumed by larval fish in Wilson Inlet indicates that the different feeding patterns among larval species probably resulted from behavioral differences (Bremigan and Stein,1994). These patterns, which occurred despite the high concentrations of zooplankton, may enhance survival, and hence recruitment, if marginally low concentrations of zooplankton were present at temporal or spatial scales beyond those sampled.

Evaluation of methods

In this study, we examined a technique for assessing DNO that consists of two parts (accounting for zooplankton abundance in the calculation of DNO and objectively assessing significance of DNO with bootstrapping). This technique was substantially more conservative than that which did not consider zooplankton abundance and which did subjectively assess significance. Prevalence of significant DNO thus doubled (32.6% to 65.1%) when zooplankton data were not included in the calculations and an arbitrary cutoff point of 0.6 was used to test for significance. The less conservative techniques of measuring DNO and assessing its significance would have therefore overestimated the degree of DNO among fish larvae in Wilson Inlet.

A large overestimation of DNO would likely have led to a different interpretation of the data. For example, the higher rate of significant overlap may have led to the conclusion that competition for food was sufficiently high to influence markedly the survival rate of fish larvae in Wilson Inlet. In contrast, the lower prevalence of overlap is more consistent with our previous hypothesis that food is unlikely to be limiting for the open-water assemblage of larval fish in Wilson Inlet (Gaughan and Potter, 1995).

Although concentrations of potential zooplankton prey are not necessarily directly related to their availability, we suggest that inferences regarding competition for food among larval fish may be misleading if data on the abundance of the zooplankton are not considered when measuring DNO. In studies of other taxa, or even of adult fish, where the abundances of prey in the environment may be very difficult or impossible to estimate without bias, resource availability can be estimated in a circular manner with proportional-utilization data (see Winemiller and Pianka, 1990). However, because the majority of fish larvae and their potential prey are planktonic, small, and relatively immobile (thus highly susceptible to capture with plankton nets), estimates of prey concentrations in the environment should be used to calculate DNO for larval fish. Likewise, because a subjective assessment of the significance of DNO is inadequate, bootstrapping techniques may prove to be useful in making an objective examination of dietary relations,which are typically awkward to analyze statistically (Winemiller and Pianka, 1990; Baltanás and Rincón, 1992).

Finally, although the two parts of the technique used in this study, i.e. objectively assessing significance and accounting for zooplankton abundance, each contributed to the overall result, individually the former had a greater influence (18.6% and 20.9%) on the estimated prevalence of significant DNO than the latter (11.6% and 13.9%). Even though the direction and magnitude of the differences between the two parts of this technique may apply only to the current study, this finding further suggests that both the incorporation of prey abundance data and an objective assessment of significance need to be considered in an analysis of dietary overlap because either may have more influence on the apparent prevalence of significant DNO.

Acknowledgments

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Abstract.—Aspects of the life history of red porgy from the South Atlantic Bight (SAB) were examined for four periods (1972–74, 1979–81, 1988–90, and 1991–94), and annual changes in the age and growth of red porgy were described for data collected during 1988–94. The life history of red porgy during 1972–74 was assumed to represent that of an unfished population, although this population had been subject to light fishing pressure. From 1972–74 to 1979–81, the back-calculated size-at-age increased slightly for ages 2–8. By 1988–90 and 1991–94, however, the back-calculated size-at-age for the same age classes was significantly smaller than that in 1979–81. In addition, size-at-maturity and size-at-sexual-transition occurred at progressively smaller sizes for 1988–90 and 1991–94. The mean size-at-age (observed and back-calculated) declined for most ages between 1988 and 1994. Von Bertalanffy growth curves fitted to the mean back-calculated size-at-age for each year showed similar decreasing trends. Changes in life history may be a response to sustained 20-year overexploitation that has selectively removed individuals predisposed towards rapid growth and larger size.

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Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972–1994*

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The red porgy, *Pagrus pagrus*, is a protogynous sparid distributed throughout the Atlantic Ocean and Mediterranean Sea at depths of 18 to 280 m (Manooch and Hassler, 1978; Vassilopoulou and Papaconstantinou, 1992). In the South Atlantic Bight (SAB) off the southeastern coast of the United States, red porgy are commonly associated with sponge or coral habitat (or both) with rocky outcrops and rocky ledges (Grimes et al., 1982), frequently referred to as "live bottom." Areas of live bottom are distributed patchily throughout the SAB, and patch size can range from square meters to square kilometers (Powles and Barans, 1980). Nevertheless, red porgy in the SAB are thought to constitute a single stock (Manooch and Huntsman, 1977).

Red porgy are an important segment of the commercial fisheries of the SAB, averaging 6% of the snapper-grouper landings since 1978 (SAFMC[1]). Similarly, red porgy make up a considerable portion of the recreational harvest of reef fishes in the SAB (Huntsman et al.[2]). The fishery for red porgy in the SAB has, however, experienced a serious decline in landings since 1982 (Vaughan et al., 1992; Huntsman et al.[2]), as well as a decline in fishery-independent catch per unit of effort (CPUE) (Fig. 1). Estimates of stock size derived from virtual population analysis (VPA) showed a peak population size in 1975 and a steady decline through 1992 (Vaughan et al., 1992; Huntsman et al.[2]). Although estimates of stock size derived from fishery-independent CPUE for 1993–1995 suggest a slight population recovery (Harris, personal obs.), the spawning stock ratio, estimated at 18% in 1993, is still considerably below the 30% level used by the South Atlantic Fishery Management Council to define when a species is overfished (Huntsman et al.[2]).

Apart from a size limit instituted in 1992, management of the fishery has remained essentially unchanged, in spite of an apparent continual decline of the resource. The ability of fishermen to locate good fishing areas (i.e. patches of live bottom) precisely using LORAN-C and Global Positioning Systems technology and

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[1] SAFMC. 1991. Amendment 4, regulatory impact review and final environmental impact statement for the snapper grouper fishery of the South Atlantic Region. South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC, 225 p.

[2] Huntsman, G. R., D. S. Vaughan, and J. C. Potts. 1993. Trends in population status of the red porgy *Pagrus pagrus* in the Atlantic Ocean of North Carolina and South Carolina, USA, 1971–1992. South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC 29422.

an increase in the number of vessels participating in the snapper-grouper fishery in the SAB resulted in a steadily increasing fishing mortality from 1972 through 1993 (Huntsman et al.[2]). For new management regulations to be considered, current life history data need to be made available. The most recent published discussion of SAB red porgy life history was based on data collected between 1972 and 1974 (Manooch, 1976; Manooch and Huntsman, 1977).

It has been shown that age structure, size-at-age, and reproductive strategies of a population will change in a predictable fashion that responds to declining abundance (Lack, 1968; Rothschild, 1986). There is, however, concern over the extent and permanence of these changes (Edley and Law, 1988; Bohnsack, 1990). The effect of sustained heavy exploitation, combined with current management strategies in regard to particular size restrictions and quotas or bag limits on the life history of a fished stock, is poorly documented. Staff of the Marine Resources Monitoring, Assessment, and Prediction Program (MARMAP), a federally funded program based at the South Carolina Department of Natural Resources in Charleston, SC, have collected life history data on red porgy since 1979. When combined with data collected from 1972 through 1974 (Manooch, 1976; Manooch and Huntsman, 1977), data spanning 24 years were available to determine if the life history of the red porgy population in the SAB had changed.

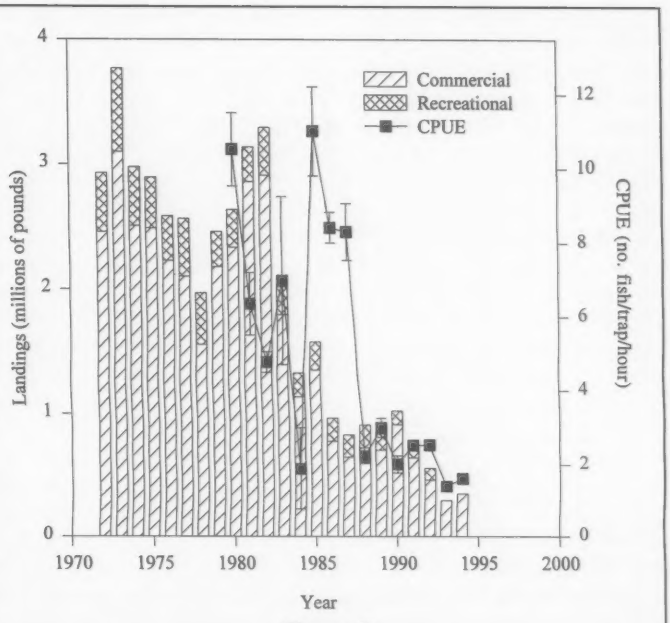

Figure 1

Commercial and recreational landings of red porgy since 1972. Recreational landings are from headboat surveys conducted by the Beaufort Laboratory of the National Marine Fisheries Service (70%), and the Marine Recreational Fisheries Statistics Survey (30%). CPUE = MARMAP trap catch per unit of effort.

Long-term life history data and the increase in fishing pressure provide a mechanism to test the impact of sustained exploitation on the life history of a reef fish species in the SAB. Therefore, the objectives of this paper were to describe temporal changes in the age, growth, and reproduction of red porgy for four periods during 1972–94 and to identify annual changes in age and growth that occurred during 1988–94.

Methods

Red porgy were collected from 1979 to 1994 during standard MARMAP sampling with chevron traps, hook-and-line gear, Florida traps, and blackfish traps (Collins, 1990; Collins and Sedberry, 1991) in the SAB from Cape Fear, North Carolina, to Cape Canaveral, Florida. Specimens were collected during daylight hours primarily between May and August of each year.

MARMAP sampling strategies changed slightly between 1979 and 1994. From 1979 to 1987, samples were collected randomly from four large areas of live bottom (identified by using underwater television) with hook-and-line gear, blackfish traps, and Florida traps to follow trends in the abundance of the various species. Additional sites outside these areas were sampled as time and weather conditions allowed (see Collins and Sedberry, 1991). Traps were baited with cut clupeids, buoyed off the research vessel, and soaked for one to four hours. Hook-and-line gear consisted of bandit reels (commercial bottom-fishing hook-and-line gear) or rod and reel with 6/0 Penn Senator high-speed reels and Electramate electric motors. Terminal gear always consisted of three hooks fished vertically and baited with cut squid or cigar minnow (*Decapterus* sp.). All fishes caught were measured (mm fork length [FL]), and the total weight for each species, from each collection, was recorded (g). All red porgy collected during these years were kept for life history studies.

In 1988 and 1989, a chevron trap was added to the gear used to sample reef fishes. During these years, the research vessel was anchored over a known live

bottom area that was verified with underwater television. Each of the three trap types (blackfish, Florida, and chevron) was deployed either from the bow, stern, or midships of the research vessel (see Collins, 1990). Hook-and-line collections were taken with rod and reel and with the three-hook terminal rig. Fishes were processed as described for 1979–87. All red porgy collected in 1988 and 1989 were kept for life history studies.

Based on the data collected during 1988 and 1989, a decision was made to discontinue the use of blackfish and Florida traps in 1990 because chevron traps sampled a greater species diversity (Collins, 1990). During the late 1980's, all live bottom locations identified during underwater television surveys and from sampling in previous years were plotted with LORAN-C coordinates to the nearest 0.1 μs and included in a sample site database. Currently, there are over 2,500 live bottom sites in the MARMAP database, from which 300–600 randomly chosen sites have been sampled each year since 1989. In addition, since 1989, the SAB has been stratified on the basis of latitude. Zone 1 includes all sites sampled south of 32°N, zone 2 all sites between 32°N and 33°N, and zone 3 all sites north of 33°N. Buoyed chevron traps were deployed from the research vessel and soaked for approximately 90 minutes. Hook-and-line (rod-and-reel) collections were made for 30 minutes at dawn or dusk. All fishes sampled were processed as in previous years. Because of concerns about potential gear selectivity, the length frequency of all red porgy caught by all four gear types during 1988 and 1989 was compared.

Since 1989, fork lengths (cm) and total weight (10 g) were recorded for all red porgy sampled in each zone for each year with a Limnoterra FMB-IV electronic fish measuring board and a Toledo electronic scale interfaced with a XT-type personal computer. In 1990 and 1994, all red porgy collected during sampling were used for life history studies. In 1991–93, up to 15 fish from each 1-cm size class and all fish larger than 350 mm FL were kept from each zone for life history studies. Red porgy used for life history studies were measured to the nearest mm (total length [TL], FL, and standard length [SL]) with a Limnoterra FMB-IV electronic fish measuring board interfaced with a XT-type personal computer. Individual weights were measured to the nearest gram with a triple beam balance.

Age and growth

Sagittae were removed at sea and stored dry. In the laboratory, the whole right otolith was immersed in cedar wood oil and examined for annuli (one translucent and one opaque zone) (Manooch and Huntsman, 1977) with a dissecting microscope with incandescent reflecting light and an ocular micrometer (1979–87) or with a dissecting microscope and reflected light from a fiber-optic light source (1988–94). The latter microscope had an attached Hitachi KP-C550 video camera connected to a personal computer equipped with a MATROX frame grabber and OPTIMAS image analysis software. The digitized image was viewed on a television monitor, and annuli were measured with OPTIMAS software. For both systems, measurements were taken from the core of each otolith to the outer edge of each opaque zone and to the edge of the otolith on a straight line midway between the posterodorsal dome and the most posterior point on the otolith (Frizzel and Dante, 1965). Annuli on this plane were consistently clearer and easier to enumerate, especially for older fish. For years where large numbers of red porgy were collected, a minimum of 350 randomly chosen fish were aged per year. All fish larger than 350 mm (FL) were aged for all years. The first reader collected measurements from all otoliths, whereas the second reader counted increments from a randomly chosen 35% of otoliths for each year. If agreement between the two counts was less than 90% for any year, the second reader read all otoliths for that year. When counts differed, otoliths were reread by both readers and discarded from further analyses if a difference in readings persisted.

Back-calculated lengths-at-age were computed by using the scale proportional hypothesis (Francis, 1990):

$$L_i = -(a/b) + (L_c + a/b)\,(O_i / O_c),$$

where L_i = length at the formation of the ith increment;
O_i = otolith radius at the formation of the ith increment;
O_c = otolith radius at the time of capture;
L_c = fish length at the time of capture;
a = intercept of otolith radius on fish length regression;
b = slope of the otolith radius on fish length regression.

Lengths were backcalculated to the most recently formed increment for comparisons of annual growth (1988–94) and to all increments for comparisons between periods (1979–81, 1988–90, and 1991–94). The SigmaPlot curve-fitting module with the Marquardt-Levenburg algorithm was used to fit von Bertalanffy growth curves to the mean back-calculated length-at-age for each year or period (SigmaPlot, 1994).

Because red porgy are protogynous sparids, and undergo a size- and behavior-related transition from

females to males, no comparison of size-at-age or growth rates were undertaken for the sexes separately. Life history data collected during four periods (1972–74, 1979–81, 1988–90, and 1991–94) were compared. The first study (1972–74) used red porgy sampled from headboats operating from North and South Carolina (see Manooch, 1976; Manooch and Huntsman, 1977). Specimens were collected throughout the year and gonads from 736 fish were examined macroscopically to assess sex and stage of maturity (Manooch, 1976). Scales from 3,278 individuals were examined to determine ages, and 222 fish were aged from whole otoliths (Manooch and Huntsman, 1977).

Red porgy collected during 1979–81, 1988–91, and 1991–94 were grouped by period. Otolith radius to fork length least-squares regressions were fitted separately for each period (except that of 1972–74) owing to concerns about temporal changes in somatic growth. Von Bertalanffy growth curves (von Bertalanffy, 1938) were fitted to the mean back-calculated size-at-age for each of the four study periods. Size-at-age was backcalculated for all increments measured. Mean observed and back-calculated sizes-at-age were compared between periods for each age with a single-factor ANOVA. Size and age distributions and size-at-age were compared between the three latitudinal zones sampled with single factor and two-way ANOVA's. It appeared from observations during sampling that larger fish may be associated with the shelf break; therefore size and age distributions, and size-at-age were also compared for different depths. Because the shelf break is located at about 48 m, two depth zones—0 to 45 m and 46 to 90 m—were compared. The same tests were performed in comparing annual data collected between 1988–94.

Reproduction

The posterior portion of the gonads of red porgy from 1979 to 1994 was removed from the fish and fixed in 10% seawater formalin for 1–2 weeks, then transferred to 50% isopropanol for 1–2 weeks. Gonad samples were processed with an Auto-Technicon 2A Tissue Processor, vacuum infiltrated, and blocked in paraffin. Three transverse sections (6–8 μm thick) were cut from each sample with a rotary microtome, mounted on glass slides, stained with double-strength Gill haematoxylin, and counter-stained with eosin y. Sex and reproductive state were assessed by one reader according to histological criteria (Table 1). Specimens with developing, ripe, spent, or resting gonads were considered sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the yolk vesicle stage and specimens with beta, gamma, or delta stages of atresia. Sex ratios, size-at-first-maturity, and the percent of mature females by 20-cm size class were calculated for all functional males and females, 1989–94. Sex ratio, size-at-first-maturity, and the percent of mature females were determined by size class for 1979–81, 1988–90, and 1991–94, and chi-square (χ^2) analysis was used to determine if there were significant differences in the proportion of males to all fish collected during the three periods and if there were differences in size-at-maturity between periods.

Results

1979–1994

A total of 20,756 (13,120 during 1972–74) red porgy were sampled during the four periods, of which 4,503 were aged and 4,293 sexed and staged (Table 2). The mean FL of fish collected from 1979 to 1994 showed a declining trend; however, there was no trend in mean age (Table 2). Increment formation was assumed to be annual (Collins et al., 1996; Manooch and Huntsman, 1977).

Age and growth

The mean observed size-at-age declined markedly from 1972–94 through 1991–94. Except for fishes aged 2–8 yr collected during 1979–81, the mean sizes-at-age for all ages for the three periods between 1979 and 1994 were smaller than those during 1972–94 (Fig. 2). The observed sizes-at-age in 1988–90 and 1991–94 were significantly smaller than those during 1979–81 ($P<0.01$) for ages 2 through 8. Red porgy aged 3 through 5 collected during 1991–94 were also significantly smaller than fish of the same age collected during 1988–90 ($P<0.01$). We were unable to include data collected by Manooch and Huntsman (1977) in our statistical analyses. The mean back-calculated size-at-age showed trends similar to the mean observed size-at-age (Fig. 3). Fish aged 2–8 were significantly smaller during 1988–90 and 1991–94 than during 1979–81, and fish aged 2–5 significantly smaller in 1991–94 than in 1979–81 and 1988–90.

The von Bertalanffy growth curves derived from mean back-calculated lengths for each period (Fig. 4) showed similar trends. The theoretical mean maximum fork length (L_∞) declined by 100 mm from 1972–74 to 1991–94 (Table 3). The theoretical growth rate (k) was higher between 1991 and 1994 than between 1972 and 1974. This difference is a reflection of the large decline in L_∞, rather than an increase in growth

Table 1

Histological criteria developed by MARMAP (Charleston, SC) to determine reproductive stage in red porgy, *Pagrus pagrus* (see D'Ancona, 1949, 1950; Wallace and Selman, 1981; Alekseev, 1982, 1983; Hunter et al., 1986; Sadovy and Shapiro, 1987; Matsuyama et al., 1988; West, 1990; Roumillat and Waltz[1]).

Reproductive state	Male	Female
Immature (virgin)	No primary males found. Juveniles were either females or, infrequently, simultaneous or transitional (see below).	Previtellogenic oocytes only; no evidence of atresia. In comparison with resting female, most previtellogenic oocytes <80 μm, area of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles and are not as elongate, germinal epithelium along margin of lamellae is thicker, ovarian wall is thinner.
Developing	Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and dorsomedial sinuses.	Oocytes undergoing cortical granule (alveoli) formation through nucleus migration and partial coalescence of yolk globules.
Running and ripe	Predominance of spermatozoa in lobules and dorsomedial sinuses; little or no occurrence of spermatogenesis.	Completion of yolk coalescence and hydration in most advanced oocytes. Zona radiata becomes thin. Postovulatory follicles sometimes present.
Developing, recent spawn	Not assessed.	Developing stage as described above as well as presence of postovulatory follicles.
Spent	No spermatogenesis; some residual spermatozoa in lobules and sinuses.	More than 50% of vitellogenic oocytes with alpha- or beta-stage atresia.
Resting	Little or no spermatocyte development; empty lobules and sinuses.	Previtellogenic oocytes only; traces of artresia. In comparison with immature female, most previtellogenic oocytes >80 μm, area of transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongate and convoluted, germinal epithelium along margin of lamellae is thinner, ovarian wall is thicker.
Mature specimen, stage unknown	Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive stage.	Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive stage.
Simultaneous (bisexual)	Presence of distinct ovarian and testicular regions in approximately equal amounts and of the same reproductive state. This gonad structure was infrequently observed in both juvenile and adult fish.	
Transitional	Ventrolateral proliferation of active testicular tissue (spermatogonia through spermatozoa) along the outer surface of the ovarian wall in spent or resting ovary (functional protogyny) or immature ovary (juvenile protogyny). As testicular tissue envelopes regressing ovary, ovary collapses laterally and sperm sinuses form within former ovarian wall.	

[1] Roumillat, W. A., and C. W. Waltz. 1993. Biology of the red porgy, *Pagrus pagrus*, from the southeastern United States. MARMAP Final Data Report, South Carolina Department of Natural Resources, Charleston, SC, 38 p.

rate (i.e. the negative relation between L_∞ and k). However, k was highest for the 1979–81 period, when L_∞ was also still relatively high.

Reproduction

Our examination of 4,293 gonads (n=1,397, 1979–81; n=727, 1988–90; n=2,169, 1991–94) revealed that sexual transition was occurring at smaller sizes in the later periods. There was a significant increase (P<0.001) in the number of males with time (Table 4). However, in 1988–90 and in 1991–94, the proportion of males to the total number of fish sexed was significantly greater at smaller sizes than during 1979–81 (Table 4). At 301–350 mm TL, male red porgy made up 24% of the fish that were sexed dur-

Table 2

Sampling data for the four study periods 1972–74, 1979–81, 1988–90, and 1991–94.

Year	Fish sampled	No. aged	Mean fork length (mm)	Mean age (years)	No. sexed
1972–74	13,120	222	—	—	—
1979–81	1,933	1,177	293	3.07	1,397
1988–90	1,853	1,261	254	2.44	727
1991–94	3,850	1,843	257	3.062	2,169
Total	20,756	4,503	268	2.86	4,293

ing 1991–94, in contrast with 7% at the same size interval during 1979–81 ($P<0.001$; Table 4). In 1979–81, male red porgy constituted 12% of the fish examined at 351–400 mm TL compared with 32% in 1988–90 ($P<0.01$) and 49% in 1991–94 ($P<0.001$; Table 4).

Size-at-maturity of female red porgy has also changed. Female red porgy became sexually mature at smaller sizes in 1991–94 than in 1979–81. During 1991–94, female red porgy first became sexually mature at 176–200 mm TL (mean age=0.9). In 1979–81, the first mature female was at 201–225 mm TL (mean age=0.9) (Table 5). There were significantly more mature females (54%; $P<0.001$) at 251–275 mm TL (mean age=1.9) in 1991–94 than during 1979–81 (27%; mean age=1.7).

Table 3

Von Bertalanffy growth equation parameters derived from the mean back-calculated fork length for each time period.

Parameter	1972–74	1979–81	1988–90	1991–94
k	0.226	0.343	0.273	0.281
L_∞	459.3	391.4	382.7	356.4

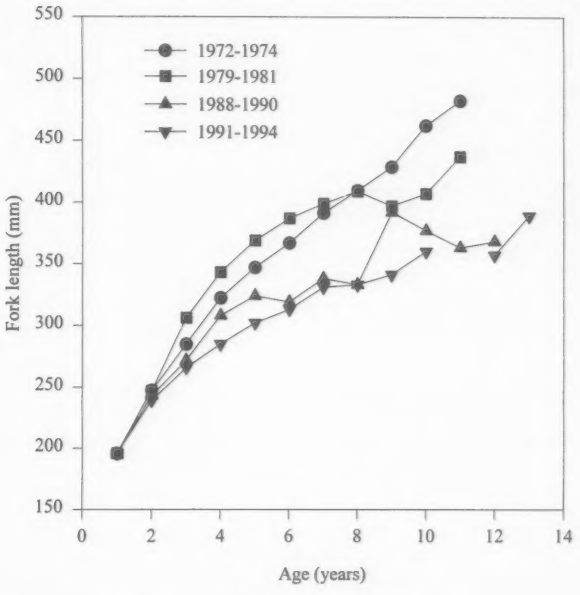

Figure 2

The mean size at capture for red porgy collected in 1972–74, 1979–81, 1988–90, and 1991–94. Ages for red porgy collected between 1972 and 1974 were taken from Manooch and Huntsman (1977).

1988–1994

A total of 2,629 live bottom stations and 5,265 red porgy were sampled May through August 1988–94, of which 4,349 specimens were kept for life history studies (Table 6). The majority of the samples were collected with chevron traps. During 1988 and 1989, there was no difference between the size range of red porgy collected in chevron traps and the size range of red porgy collected in blackfish traps, Florida traps, hook-and-line gear, or all three of these gear types combined (Fig. 5). Similarly, there was no difference in the size range of red porgy sampled by hook-and-line gear and chevron traps between 1990 and 1994 (Fig. 5). Between 1988 and 1991, however, the mean size of red porgy captured with hook and line was significantly larger each year than the mean size of porgy taken with the remaining gear types ($P<0.05$), although there was no significant difference between mean size of fish captured with the gear types used in 1993 and mean size of fish captured with the gear types used in 1994. The size of red porgy sampled during 1988–94 ranged from 90 to 501 mm FL. The mean size was 256 mm FL, with the highest frequency occurring at 240 mm FL. The length frequency of aged red porgy was very similar to the length frequency of all red porgy sampled.

Age and growth

Ages were obtained for 2,935 (67%) of the red porgy otoliths collected (Table 6). Agreement between the first and second reader averaged 93%, and was never less than 90% for any year. The mean observed size-at-age declined for most ages between 1988 and 1994 (Table 7), although there was a significant increase in the mean age of red porgy over the study period (Fig. 6; $P<0.01$; $r^2=0.94$). The mean observed size-at-age for red porgy 2 years and older sampled during 1988 and 1989 was significantly larger than all other years, with the mean observed size-at-age in 1992 and 1993 consistently the smallest (Table 7; Fig. 7). Above age 6, growth rates appeared to taper off sharply for all years (Fig. 7). Age-6 red porgy collected during 1988 had the third highest mean length recorded for all age classes in any year. Similar to the mean observed size at age, mean back-calculated size at the most recent annulus was significantly larger for 1988 and 1989 compared with other years for ages 2 and greater and also appeared to reach asymptotic size at age 6 for each year (Table 8; Fig. 8).

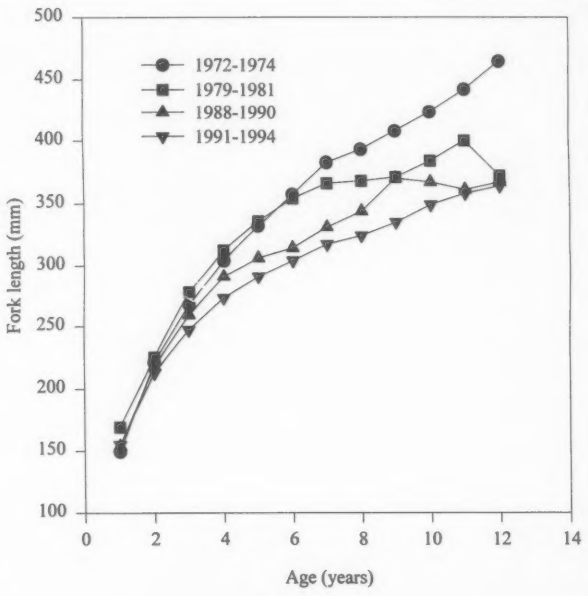

Figure 3

The mean back-calculated size at age for red porgy collected in 1972–74, 1979–81, 1988–90, and 1991–94. Back-calculated lengths for red porgy collected between 1972 and 1974 were derived from scale ages.

The von Bertalanffy growth curves fitted to the mean back-calculated size at most recent age (ages 1–10) for each year demonstrated some differences between years (Fig. 9), with growth curves from 1988 and 1989 showing larger fish at age, and higher L_∞ and k. Both k and L_∞ tended to decrease during the study period, although neither of these trends were significant (linear regression; $P>0.05$; Fig. 10).

No significant differences were apparent in size distribution, age distribution, or size-at-age between

Table 4

Percentage of male red porgy relative to the total number of individuals sexed during 1979–81, 1988–90, and 1991–94. A significant difference (χ^2; $P<0.01$) in the proportion of males for a particular size class collected during 1979–81 is denoted by *"A"*. A significant difference (χ^2; $P<0.01$) in the proportion of males that were collected during 1988–90 is denoted by *"B"*.

	1979–81			1988–90			1991–94		
Size (mm TL)	Total	Males	%Males	Total	Males	%Males	Total	Males	%Males
<200	19	—	—	16	—	—	57	—	—
200–250	216	—	—	140	2	1.43	372	4	1.08
251–300	271	10	3.69	163	5	3.07	491	33	6.72^{B}
301–350	313	21	6.71	226	25	11.06	814	194	23.83^{AB}
351–400	239	29	12.13	136	44	32.35^{A}	371	183	49.33^{AB}
401–450	160	38	23.75	38	17	44.74^{A}	57	25	43.86^{A}
451–500	158	108	68.35	8	4	50.00	6	4	66.67
501–550	18	12	66.67	—	—	—	1	—	—
551–600	2	1	50.00	—	—	—	—	—	—
Total	1,397	220		727	97		2,169	443	

the three latitudinal zones. However, significant differences were apparent in the size and age distribution between the two depth zones ($P<0.05$), with larger and older fish occurring in the deeper zone. There were no significant differences in the size-at-age between these two zones ($P>0.05$).

Discussion

Samples were collected from throughout the SAB during 1988–94. However, 69% of the collections and 73% of the aged red porgy were taken from zone 2 (32°N–33°N). Zone 2 was sampled most frequently because it was most accessible from Charleston, South Carolina, the base of operations (latitude 32° 45'N). Once settled, red porgy do not appear to move very much (Parker, 1990) and could experience differential growth rates because of differing environments. Therefore the concentration of sampling in zone 2 could have resulted in biased estimates of size-at-age. However, the comparison of size-at-age of red porgy showed no significant differences between latitudinal or depth zones; therefore, although there may be localized differences in growth rates, perhaps associated with different patches of live bottom, the mean growth rate appears to be similar throughout the region. The mean depth and temperature of areas sampled in the MARMAP surveys have not changed significantly since 1987; thus these environmental variables, at least, have not caused the life history changes in red porgy (Fig. 11).

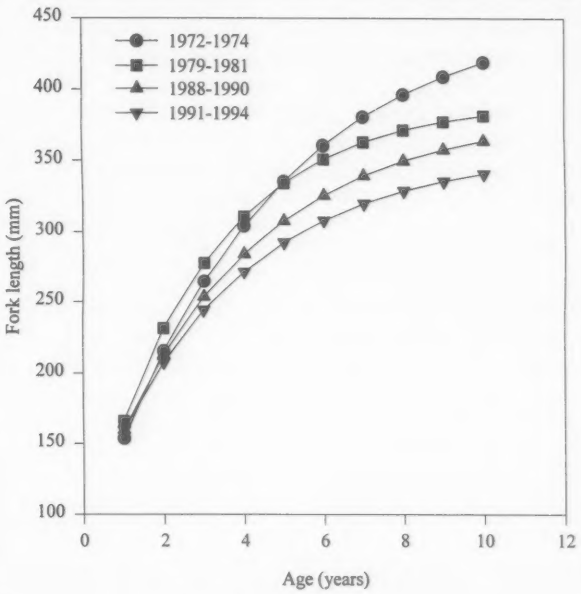

Figure 4

The von Bertalanffy growth curves derived for red porgy collected in 1972–74, 1979–81, 1988–90, and 1991–94. The von Bertalanffy growth curve for red porgy collected between 1972 and 1974 was derived from scale ages.

There were significant differences in size and age by depth, with larger and older fish occurring in deeper water. This difference may be due to fishermen operating in deeper water with larger hooks and baits to target groupers, thus reducing the availability of this gear to red porgy, particularly to smaller

Table 5

Percentage of red porgy females that were sexually mature relative to all females collected during 1979–81 and 1991–94. A significant difference (χ^2; $P<0.01$) in the proportion of mature females is denoted by "A".

	1979–81			1991–94		
Size (mm TL)	Total females	Number mature females	Percent mature females	Total females	Number mature females	Percent mature females
<200	16	—	—	55	2	3.64
200–225	91	1	1.10	182	4	2.20
226–250	85	11	12.94	156	26	16.67
251–275	103	28	27.18	157	85	54.14[A]
276–300	78	77	98.72	211	189	89.57
>300	512	512	100.00	615	606	98.54
Total	885	62	1,376	912		

individuals. Therefore, red porgy in deeper water may experience reduced fishing mortality in comparision with those in shallower waters. In shallower water, fishermen reduce hook and bait size to catch smaller fishes, and more red porgy of all sizes are landed. Alternatively, the increase in size and age with depth

Table 6

Sampling data for 1988–94, collected from the RV *Oregon* (1988–89) and the RV *Palmetto* (1990–94).

Year	Trap collections	No. porgy	Hook-and-line collections	No. porgy	No. processed	No. aged
1988	84	294	261	170	427	371
1989	65	248	198	174	388	345
1990	348	957	111	44	997	545
1991	306	830	33	25	519	426
1992	324	1,107	25	1	494	419
1993	414	722	52	45	538	385
1994	370	1,107	38	11	986	444
Total	1,911	5,265	718	470	4,349	2,935

Table 7

Mean observed fork length (mm) at age for red porgy (standard error in parenthesis).

Age (yr)	1988	1989	1990	1991	1992	1993	1994
1	191 (2) *n*=124	203 (3) *n*=70	197 (3) *n*=78	200 (2) *n*=126	190 (2) *n*=78	206 (3) *n*=70	186 (1) *n*=53
2	256 (2) *n*=107	248 (2) *n*=149	234 (2) *n*=218	237 (2) *n*=110	228 (2) *n*=119	245 (3) *n*=78	253 (2) *n*=101
3	284 (3) *n*=95	284 (4) *n*=54	264 (2) *n*=180	274 (3) *n*=71	261 (3) *n*=72	267 (3) *n*=104	264 (3) *n*=50
4	328 (7) *n*=26	305 (5) *n*=39	295 (5) *n*=26	282 (4) *n*=70	287 (3) *n*=64	290 (4) *n*=59	283 (3) *n*=106
5	386 (34) *n*=2	328 (6) *n*=18	314 (10) *n*=16	303 (8) *n*=17	305 (4) *n*=43	308 (5) *n*=35	297 (3) *n*=86
6	334 (7) *n*=4	305 (34) *n*=3	317 (13) *n*=5	335 (7) *n*=13	310 (7) *n*=14	305 (5) *n*=25	313 (5) *n*=32
7	374 (10) *n*=5	340 (35) *n*=3	308 (7) *n*=6	339 (20) *n*=5	321 (7) *n*=8	359 *n*=1	334 (5) *n*=9
8	352 (3) *n*=4	335 *n*=1	307 (9) *n*=3	322 (5) *n*=4	328 (5) *n*=2	348 (25) *n*=6	324 (6) *n*=4
9	389 *n*=1	394 (42) *n*=2	384 (17) *n*=2	362 *n*=1	344 (8) *n*=6	322 (18) *n*=2	
10		372 (28) *n*=2		361 (16) *n*=4		344 (7) *n*=2	390 *n*=1
11		363 *n*=1					
12		368 *n*=1			360 *n*=1	354 *n*=1	
13					390 (9) *n*=2		

could reflect a gradual movement of red porgy towards deeper water as they age. Grimes et al. (1982) suggested that red porgy associated with shallow reefs may temporarily move to deep water in response to unusually cold water temperatures. However, tagging studies have shown that settled red porgy undertake very little long-term movement (Grimes et al., 1982; Parker, 1990). Another reef species, black sea bass (*Centropristis striata*), has shown limited movement of larger fish to deeper water (Ulrich and Low[3]; Harris and McGovern, personal obs.).

Fishing mortality (F) of red porgy has increased since 1972, although between 1972 and 1975 it showed a slight decline (Vaughan et al., 1992). The F for fully recruited ages (5–9) increased from 0.2 in 1976 to 1.3 in 1991 (Huntsman et al.[2], Murphy VPA, M=0.28). The F for ages 1–4 showed similar trends, although the magnitude of the increase was less (Huntsman et al.[2], Murphy VPA, M=0.28). Owing to the changes in the life history of red porgy since 1972, these estimates of fishing mortality are probably high; yet, the increasing trend in fishing pressure is evident. Except for an increase during 1981–83, landings of red porgy have been declining since 1973 (Fig. 1). Similarly, the number of recruits to age 1 have declined steadily since 1974 (Huntsman et al.[2], Murphy VPA, M=0.28). An estimate of SSR in 1993 was only 18% (Huntsman et al.[2], Murphy VPA, M=0.28). Again, the changes in the life history of red porgy since 1972 indicate that Huntsman et al.[2] may have underestimated the decline in the abundance of age-1 fish.

Concurrent with the fishery becoming increasingly overexploited, there has been corresponding change

[3] Ulrich, G. F., and R. A. Low. 1992. Movement and utilization of black sea bass, *Centropristis striata*, in South Carolina. Final Unpubl. Rep. NOAA Award No. NA90AA-D-FM656, 11 p.

Table 8

Mean back-calculated fork length (mm) at age for red porgy (most recent annulus; standard error in parenthesis).

Age (yr)	1988	1989	1990	1991	1992	1993	1994
1	163 (2) *n*=124	180 (3) *n*=70	173 (4) *n*=78	166 (2) *n*=126	159 (2) *n*=78	171 (2) *n*=70	161 (2) *n*=53
2	230 (2) *n*=107	233 (2) *n*=148	218 (2) *n*=218	219 (2) *n*=110	210 (2) *n*=119	227 (3) *n*=78	237 (2) *n*=101
3	266 (3) *n*=95	273 (3) *n*=54	252 (2) *n*=180	259 (3) *n*=71	246 (3) *n*=72	257 (3) *n*=104	253 (3) *n*=50
4	316 (6) *n*=26	300 (6) *n*=38	286 (5) *n*=26	271 (3) *n*=70	274 (3) *n*=64	281 (4) *n*=59	275 (3) *n*=106
5	382 (31) *n*=2	325 (7) *n*=18	304 (11) *n*=16	292 (8) *n*=17	298 (4) *n*=43	301 (5) *n*=35	291 (3) *n*=86
6	328 (7) *n*=4	301 (32) *n*=3	311 (13) *n*=5	326 (6) *n*=13	299 (7) *n*=14	298 (6) *n*=25	307 (5) *n*=32
7	369 (10) *n*=5	339 (34) *n*=3	294 (7) *n*=6	331 (18) *n*=5	313 (6) *n*=8	354 *n*=1	329 (5) *n*=9
8	347 (3) *n*=4	335 *n*=1	300 (10) *n*=3	314 (5) *n*=4	320 (4) *n*=2	351 (20) *n*=7	320 (6) *n*=4
9	389 *n*=1	392 (40) *n*=2		354 *n*=1	335 (8) *n*=6	292 *n*=1	
10		371 (27) *n*=2	378 (17) *n*=2	350 (16) *n*=4		336 (4) *n*=2	382 *n*=1
11		362 *n*=1					
12		367 *n*=1			356 *n*=1	349 *n*=1	
13					382 (8) *n*=2		

in the life history of red porgy during a 22-year period (1972 to 1994). The first study of age and growth on red porgy (1972–74) (Manooch and Huntsman, 1977) was assumed to describe a stock with the same life history as the virgin population, even though it was subject to light fishing pressure. By the late 1970's and early 1980's, the growth pattern of the stock had changed. The mean observed and back-calculated lengths-at-age as well as the von Bertalanffy growth curve for the 1979–81 period showed a larger size at age for ages 2–6 but a lower theoretical maximum size. The increase in growth rate, and resultant increase in size-at-age observed during this period, is considered a typical density-dependent response to an increase in mortality as the depressed population responds to an increased availability of resources (Pitcher and Hart, 1982; Rothschild, 1986). The decrease in theoretical maximum size between 1979 and 1981 may have resulted from the selective removal of larger individuals from the population by fishermen and not from a biological change in the theoretical maximum size that the fish could attain.

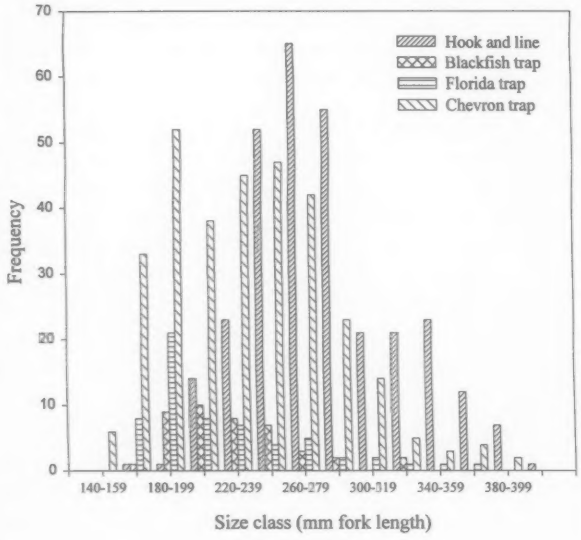

Figure 5

Length frequency for all red porgy sampled in MARMAP surveys between 1988 and 1994 by gear type.

During the mid 1980's through the early 1990's, increasing fishing pressure apparently continued the selective removal of larger, faster growing individuals from the population, further exacerbating the changes in the life history of red porgy. By 1988–90, mean back-calculated sizes-at-age were significantly smaller for all ages except age 1 in comparison with 1979–81. In 1988–90, the values of k and L_∞ were smaller than during 1979–81 and 1972–74, indicating a reduced growth rate and a lower theoretical maximum attainable size. Mean back-calculated size-at-age for specimens collected between 1991 and 1994 were significantly smaller than those collected in 1988–90, except for ages 1, 7, and 10. These temporal reductions in the size-at-age and growth rates suggest that many individuals genetically predisposed towards rapid growth and larger size may have been selectively removed from the population, leaving behind individuals that tend to be slower growing and smaller.

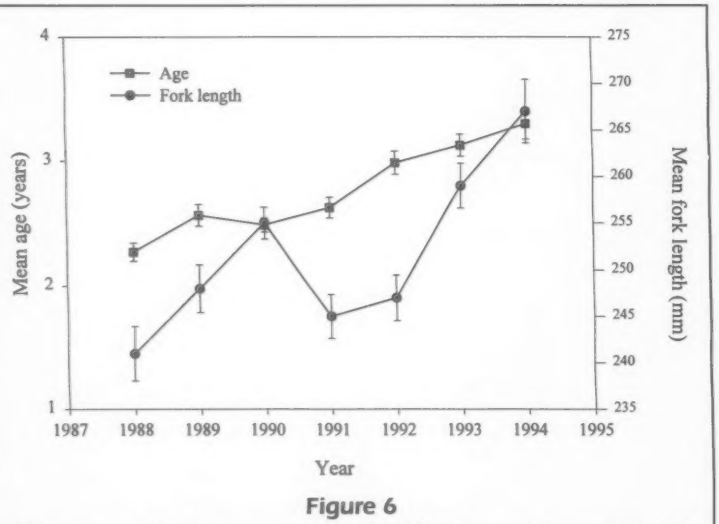

Figure 6

The mean age of red porgy sampled in MARMAP surveys between 1988 and 1994.

Red porgy also responded to the continued removal of larger individuals from the population over many generations by females becoming sexually mature at smaller sizes during 1991–94 than during 1979–81. Manooch (1976) reported that female red porgy became mature at much larger sizes than those

found in the present study. Furthermore, the red porgy population has responded to increased fishing pressure by undergoing sexual transition and by producing significantly more males at smaller sizes in recent years than during 1979–81. Koenig et al. (1996) reported that gag, *Mycteroperca microlepis*, a protogynous grouper, was undergoing sexual transition at much smaller sizes during 1991–93 in the Gulf of Mexico than were reported by Hood and Schlieder (1992) for the same region, during 1977–80. Changes in life history aspects of gag from the Gulf of Mexico were attributed to steadily increasing fishing pressure.

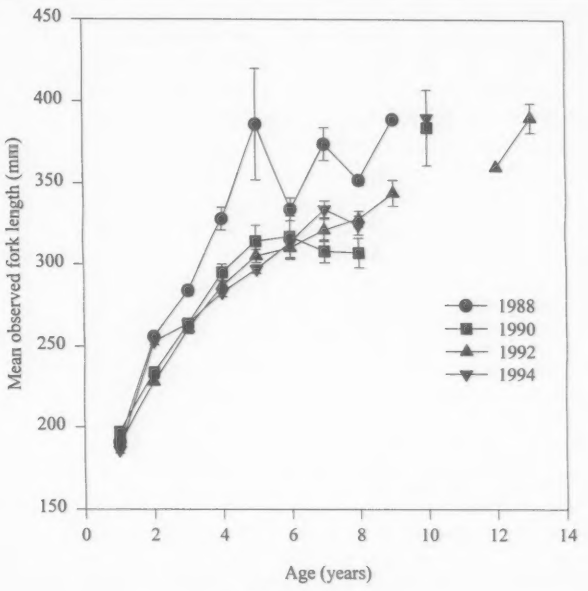

Figure 7

The mean observed size-at-age of red porgy for every second year between 1988 and 1994.

The decrease in mean size-at-age, growth rates, and size-at-maturity during 1988–1994 is probably a continuation of the changing life history pattern of the population that has resulted from sustained fishing pressure and indicates the degree of change that can occur over relatively short periods of time. These relatively rapid changes in size-at-age may reflect the inability of an overfished or depressed population to absorb or respond to further decreases in population size. Apart from the decreases in size-at-age apparent from recent years, the mean age and fork length of the population has increased since 1988. These increases may be due to a decline in the number of younger fish recruiting to the population. The net effect of fewer young fish in the population (and therefore samples) would be an increase in the mean age and size of the sampled fish. Length-frequency data collected in MARMAP surveys since 1988 indicates no strong recruiting year class (age-1) since 1990. Huntsman et al.[2] found that the estimated number of 1-year-old red porgy had declined steadily since 1973 (Murphy VPA, M=0.28); their results also indicate that the population may be experiencing a decline in recruitment.

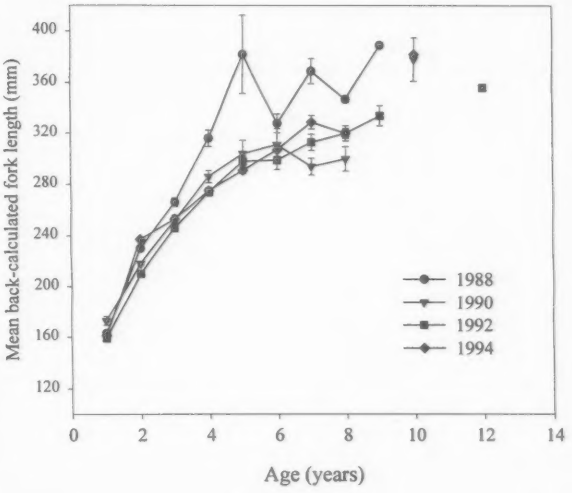

Figure 8

The mean back-calculated size-at-age for every second year between 1988 and 1994.

A decline in recruitment may be attributed to several factors that are the result of sustained overfishing. First, as the number of fish in the population declines, fewer and fewer females are available to spawn, resulting in a decline of total potential egg production (Vaughan et al., 1992; Huntsman et al.[2]). Second, decreases in size-at-maturity and size-at-age result in fish that are less fecund than larger fish (Manooch, 1976). Finally, smaller females may produce eggs that are poorer in quality than those produced by larger

females because smaller individuals put more energy into somatic growth rather than into reproductive tissue (Rothschild, 1986). Zhao and McGovern[4] found that an apparent population size threshold at 30% of the virgin spawning biomass existed for vermilion snapper (*Rhomboplites aurorubens*) in the SAB, below which recruitment failure was almost inevitable. A similar situation may exist for red porgy in the SAB, with recruitment failure exacerbated by the reduction in size of mature females.

Reproductive (i.e. recruitment) failure may also be affected by the change in size of male red porgy, as well as the changes in sex ratio that have occurred since 1972–74. Currently, some red porgy undergo transition at 200–250 mm FL. The sex ratio in 1991–94 at 352–400 mm FL was 1.3 males for each female. In 1972–74, the sex ratio for this size class was 0.06 males per female (Manooch, 1976, macroscopic sexing). Males began to outnumber females only above 451 mm FL. Koenig et al. (1996) have hypothesized that sperm limitation may be a factor in the decline of gag, *Mycteroperca microlepis*, in the northern Gulf of Mexico as the number of males in the population has declined. The size and number of male red porgy in the population have similarly been greatly reduced. The reduction in size and number of males may also be a significant factor in the decline in the number of 1-year-old red porgy recruiting to the SAB population.

Huntsman et al.[2] concluded that the red porgy population of the SAB was overfished and that the population was severely depressed. These conclusions were based on the results of Murphy and separable VPA's that used only two age length keys—one from 1972–74 and one from 1986—and that used von Bertalanffy parameters and a length-weight relation from 1972–74. The life history of red porgy has changed markedly since 1986. In fact, as this study shows, significant decreases in size-at-age have occurred within a matter of years in this heavily fished population. The dramatic changes in the life history of red porgy and the resultant changes in parameters used for stock assessment suggest the status of the population in the SAB needs to be reassessed.

Protogynous fishes may be particularly vulnerable to sustained heavy fishing pressure and size selective mortality (Huntsman and Schaaf, 1994), particularly if sex reversal occurs primarily in response to exogenous controls (sociodemographic factors) (Koening et al., 1996). The decline in size at sex transition since 1979 suggests that the timing of transition in red porgy is not determined by size, but rather by some social or behavioral stimulus.

Red porgy probably do not aggregate to spawn; instead they appear to be permanently schooled on the available areas of live bottom in the SAB. Koenig et. al. (1996) suggested that if a population of protogynous fish remained aggregated throughout the year, transition could occur year-round and thus the normal male to female ratio could be maintained. If the numerical sex ratio is maintained, the impact of overfishing on a protygynous species is reduced (Huntsman and Schaaf, 1994). The increase in the sex ratio seen from 1979–81 to 1988–90 may represent overcompensation for the depletion of males from the population. The males of many reef-associated protogynous sparids show strong territoriality (van der Elst, 1988). If these males are more aggressive and are more likely to be caught by fishermen (Koenig et. al.,

[4] Zhao, B., and J. C. McGovern. 1995. Population characteristics of the vermilion snapper, *Rhomboplites aurorubens*, from the southeastern United States. Report to the South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC 29422, 35 p.

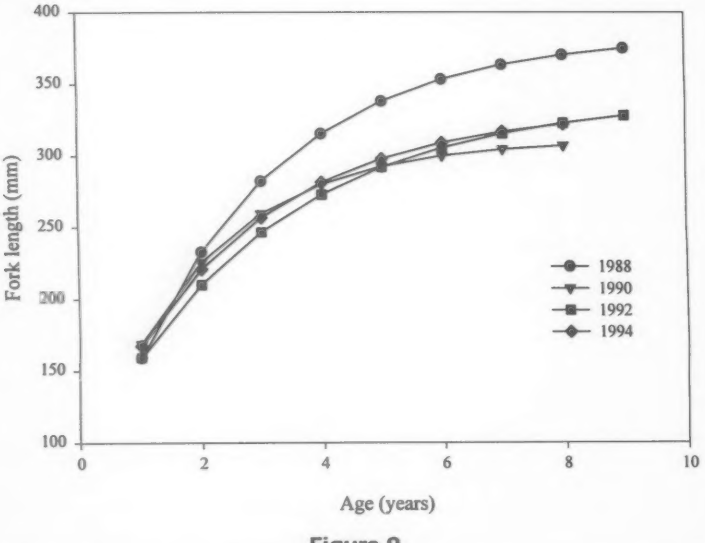

Figure 9

The von Bertalanffy growth curves for red porgy for every second year sampled since 1988.

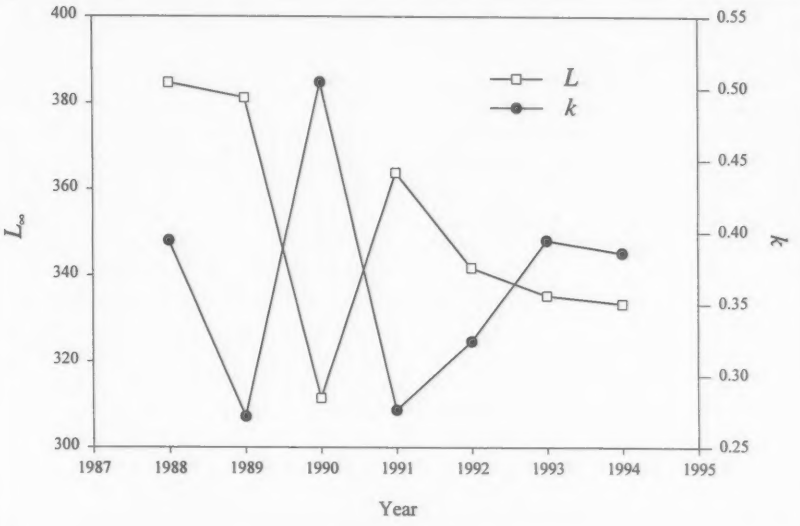

Figure 10

Trends in von Bertalanffy parameters from the growth equations derived for red porgy sampled between 1988 and 1994.

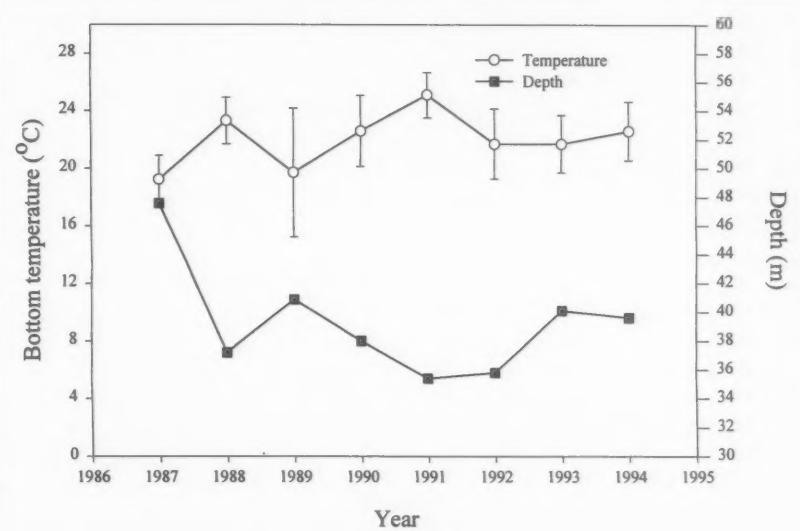

Figure 11

Mean summer bottom temperature of the South Atlantic Bight, 1987–94. Temperatures were recorded between April and October of each year.

1996; Gilmore and Jones, 1992), then another fish, presumably the largest (=dominant) female would take over that territory and begin to undergo transition (Shapiro, 1981). As modern technology allows fishermen to locate good fishing sites precisely, all large fish could be removed from an area. The increase in the number of males seen during 1988–90 may also be a function of fish size. As large males

were removed from the population, smaller fish could occupy the now vacant territory and undergo transition. As new males became increasingly smaller, the size of the territory they could successfully hold might also become smaller, freeing territory for additional males. However, as the size of the fish declined even further, it is possible that the males would be unable to compete against other species, thereby further reducing the available habitat for red porgy males and reducing the sex ratio to the same level as that found in 1979–81.

It has been hypothesized that the selective removal of individuals predisposed to rapid growth and greater size may cause a genetic shift resulting in a population of slower growing, smaller individuals than those found in the unfished population (Bohnsack, 1990; Sutherland, 1990). Edley and Law (1988) found that individuals of a population of *Daphnia magna* subjected to size-selective mortality of its large individuals for 10 generations did not return to the size and growth rates of a control population, even after the size selective pressure was removed. Changes in the life history of red porgy over the last two decades strongly confirm the hypothesis of Bohnsack (1990) and Sutherland (1990). Although exploitation may not last long enough to result in a permanent genetic shift to slower growing, smaller individuals, phenotypic changes have already occurred. Failure to consider the potential evolutionary changes that could be induced in a population through fishing mortality could result in a reduction of the maximum potential yield of that stock (Law and Grey, 1989). In addition, a reduced population of smaller red porgy could have implications in reef fish community structure, i.e. the role of smaller red porgy in a reef habitat may be different, or smaller red porgy may be less able to compete for more desirable habitat.

Current management strategies only enhance the impact of the size selective mortality associated with fisheries. In 1992, Amendment 4 of the SAFMC snapper-grouper management plan was enacted, requiring a minimum size of 12 inches (305 mm TL) for red porgy in catches (SAFMC[1]). Fishermen tend to target larger fish because these bring the largest return (economic for commercial fishermen, aesthetic for recreational fishermen). Size-at-maturity for red porgy females was 270 mm TL in 1972–74; 200–225 mm TL in 1979–81; and 175–200 mm TL in 1991–94. However, 100% maturity occurred at 350 mm TL during 1972–74 and >300 mm TL in 1991–94. Thus, many faster growing individuals may reach legal size before they are sexually mature or when they have only had the opportunity to spawn once or twice. Slower growing individuals would take longer to reach the size limit and have a greater chance to spawn before becoming available to the fishery, thus further exacerbating the effect of size-selective mortality.

The SAB population of red porgy has undergone significant changes in life history, presumably in response to sustained, long-term size-selective overexploitation. Individuals in the population are smaller, have reduced growth rates, a reduced theoretical maximum size, and undergo sexual maturity and transition at smaller sizes now than 20 years ago. The selective pressure of fishing mortality may be causing a genetic shift towards a slower growing, smaller population. Unless appropriate management measures are taken, sustained overfishing could result in a permanent genetic shift in the fish or a total collapse of the stock (or both).

Acknowledgments

The authors wish to thank the crews and scientific parties of the research vessels that made collection of these data possible. Bill Roumillat and Wayne Waltz aged, sexed, and identified maturity stages of red porgy collected between 1979 and 1987, and Oleg Pashuk sexed and staged all red porgy collected since 1987. Three anonymous reviewers provided numerous comments that improved the manuscript immeasurably.

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Reproductive success of Pacific herring, *Clupea pallasi*, in Prince William Sound, Alaska, six years after the *Exxon Valdez* oil spill

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Abstract.—The *Exxon Valdez* oil spill occurred just prior to the spring migration of Pacific herring, *Clupea pallasi*, from offshore feeding grounds to nearshore spawning areas in Prince William Sound (PWS), Alaska. Most or all of the life stages of herring in PWS may have been exposed to oil after the March 1989 spill. Delayed impacts from the spill were suspected as one possible cause in the unprecedented crash of the adult herring population in 1993 and stimulated studies to assess reproductive success. In spring 1995, mature herring were collected from four sites in PWS and from three uncontaminated sites in southeast Alaska (SE) to determine if reproductive impairment was evident in PWS herring six years after the spill. Herring were artificially spawned and their eggs were reared in a laboratory until hatching. Observed response parameters included fertilization success, hatching times, hatching success, as well as larval viability, swimming ability, and spinal abnormalities. Responses of all year classes combined or those restricted to the same year class did not differ significantly between regions ($P>0.50$); the best and worst responses generally occurred in the SE. Within each site, response of the 1989 year class (most likely impacted by the oil spill in PWS) generally did not differ significantly from any other year class. To verify macroscopic observations, a subset of larvae from the 1989 year class was also inspected microscopically for yolk and pericardial abnormalities, and yolk volume was measured—but no significant regional differences were observed for any of these morphological categories. Based on the parameters examined in this study, evidence of reproductive impairment of Pacific herring in PWS by the spill was not detected in 1995, and the chances of detecting any oil-related effects against natural background variation appeared to be negligible.

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Fishery Bulletin 95:748–761 (1997).

The *Exxon Valdez* oil spill (EVOS) in Prince William Sound (PWS), Alaska, occurred just a few weeks prior to the Pacific herring, *Clupea pallasi*, spawning season. Most or all of the life stages of herring in PWS may have been exposed to oil after the March 1989 spill. Biologically available hydrocarbons were present in the upper water column of PWS for several weeks following the spill (Short and Harris, 1996a), and residual oil may have persisted in some areas into 1990 (Short and Harris, 1996b). An estimated 40–50% of the egg biomass in PWS was deposited within the oil trajectory (Brown et al., 1996a). The failure of the 1989 year class to recruit to the fishery and the subsequent crash of the 1993 population (Meyers et al., 1994) suggested that the early life stages of herring were impacted either from exposure of prespawning adults or from direct exposure of eggs and larvae. Thus, as fish exposed to oil were recruiting into the fishery (20% by age 3, 80% by age 4, 100% by age 5; Funk[1]), the herring population crashed, and recovery was minimal through the 1996 season (Wilcock[2]). Genetic damage, physical deformities, and small size were reported for newly hatched larvae following the spill (Brown et al., 1996a; Hose et al., 1996; Norcross et al., 1996; Marty et al., in press), but long-term effects remain unknown. In a preliminary study in 1992, Kocan et al. (1996b) observed decreased reproductive success in herring from an oil-contaminated area in PWS compared with an uncontaminated area; results were inconclusive, however, because only two sites were compared. Delayed effects from the spill were suspected as one possible cause of the population decline and stimulated the

[1] Funk, F. In prep. Age-structured assessment of Pacific herring in Prince William Sound, Alaska and forecast of abundance for 1994. Regional Information Report, Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, PO Box 25526, Juneau, AK 99802-5526.

[2] Wilcock, J. 1996. Alaska Department of Fish and Game. Commercial Fisheries Management and Development Division, PO Box 669, Cordova, AK 99574. Personal commun.

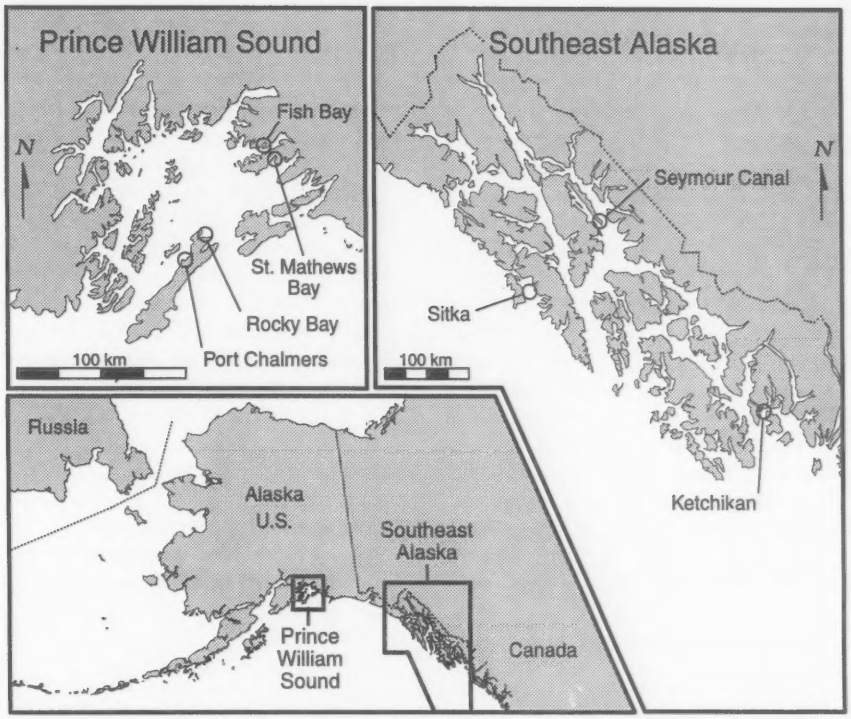

Figure 1

Collection sites of mature Pacific herring in Prince William Sound and southeast Alaska in spring 1995.

need for more definitive studies to assess the reproductive success of herring.

The purpose of this study was to determine if reproductive impairment, a possible result of the spill, was evident in PWS herring six years after the spill. There were two major focuses in the study: 1) a comparison of reproductive success between regions (PWS and southeast Alaska [SE]) and 2) a comparison of reproductive success between year classes within sites, particularly the 1989 year class (most likely impacted by the oil spill) with other year classes in PWS.

Sites sampled within PWS included all areas where spawning occurred in 1995; spawning was absent in areas that were heavily contaminated with oil in 1989. For example, Naked Island, which was in the middle of the spill trajectory, had 22 km of spawned eggs in 1989 (Brown et al., 1996a) but none in 1995. Although some have speculated that herring home to the same general spawning area each year (Zijlstra, 1963; Hourston, 1982), site fidelity is poorly understood. Thus, the herring we sampled in PWS in 1995 may or may not have been exposed to oil at some earlier time in their life history (as adults, eggs, or larvae).

Methods

Herring were collected at four sites in PWS and at three sites in SE (Fig. 1); all sites had been used for spawning in previous years. Two of the sites in PWS (St. Mathews Bay and Fish Bay) were not directly contaminated by the oil spill, whereas the other two sites (Port Chalmers and Rocky Bay) were at least lightly contaminated. Shortly after the spill, elevated hydrocarbon levels were detected in mussels at Rocky Bay (Brown et al., 1996b) and in seawater at Port Chalmers (Carls[3]). Additionally at Port Chalmers, concentrations of oil metabolites in bile of adult herring sampled in spring 1990 were similar to metabolite concentrations observed in 1989. This finding suggested continued contamination (Brown et al., 1996b). Herring were collected in St. Mathews Bay on 7 April, in Fish Bay on 14 April, at Port Chalmers on 30 April, and in Rocky Bay on 1 May 1995. In SE, herring were collected in waters off Sitka on 29–30 March, in waters near Ketchikan on 11 April, and in Seymour Canal on 13 May 1995.

[3] Carls, M. G. 1996. Prince William Sound oil database. Auke Bay Laboratory, National Marine Fisheries Service, NOAA, 11305 Glacier Hwy., Juneau, AK 99801.

Mature herring were captured during or just prior to spawning at all sites, sorted by size, and artificially spawned. Capture gear included gill net, cast net, and purse seine. Fish were chilled immediately after capture and transported within two hours to a field laboratory, except Seymour Canal fish, which were transported directly to Auke Bay Laboratory (ABL). To approximate the different age classes present, fish were sorted by sex and size (usually in 10-mm increments; e.g. 220–230 mm fork length). Six or more size classes were usually identified at each site. From each size class, 25 females were artificially spawned with males of the same size; generally 3 males contributed sperm for all 25 crosses. Size classes of fish were processed at random. Each fish was assigned an identification number, measured to the nearest mm (fork length), and weighed to the nearest 0.1 g (wet weight). To determine age, three scales were removed from the left side of each spawned fish near the posterior margin of the dorsal fin, placed on a glass slide, and covered with a second slide.

For spawning, testes were removed, sealed in a plastic bag and maintained in chilled seawater until use; ovarian membranes were cut longitudinally, and eggs were removed with a hydrocarbon-free stainless steel spatula similar to that used by Brown.[4] From each female, approximately 150 eggs were deposited with a gentle swirling motion onto a 25 × 75 mm glass slide placed on the bottom of a shallow plastic dish filled with seawater. Each slide was then placed in a staining rack and suspended in its own 1-L beaker of seawater. Milt was prepared from collected testes by cutting sections from each into small segments; segments plus a small amount of seawater were mixed with a spatula. A few milliliters of the milt mixture were added to each beaker containing eggs. Eggs and milt remained in contact for 5 min; the milt was then poured off, and the eggs were gently rinsed in seawater. Slides were kept in staining racks and maintained in ambient seawater with constant aeration until they were transported to ABL by air. To transport the eggs, staining racks were placed in plastic seawater-filled containers, which were then placed in coolers with blue ice.

Slides with eggs from each site were randomly distributed among twelve 600-L tanks with flow-through seawater. Slides were suspended from monofilament line attached to a pivoting overhead framework designed to cause slow egg movement (1 rpm) through the water. During the first 16–18 days of incubation, all slides were maintained in the seawater bath. A few days before hatching, each slide was isolated in a 1-L glass jar that contained seawater and that was surrounded by flowing seawater. Lighting was natural, supplemented by overhead fluorescent light during daylight hours. Seawater flow was approximately 1 L/min at 3.9°C, warming to 7.1°C with normal seasonal change. Salinity was 32 ±1 ppt.

Reproductive success of female herring was defined as the production of physically and functionally normal larvae. Key reproductive parameters included hatching success and larval viability, swimming ability, and spinal abnormalities. These four parameters were sensitive to oil in laboratory studies (Carls et al.[5]). Other parameters examined included fertility and hatching times. Fertility was not considered a key parameter because it may have been negatively influenced by unavoidable handling conditions at the different sites and by variable periods in the storing of gametes prior to spawning. Hatching times were not considered a key parameter because they were strongly influenced by seasonal increases in water temperature.

Fertilization success and stage of development were determined 1 to 10 days after spawning. Excess eggs were removed from all slides by scraping—i.e. those along slide margins susceptible to mechanical damage and clumps of eggs not directly exposed to water. This process was accomplished in water with minimal exposure to air.

Isolated eggs were inspected every two days to determine onset of hatching. Once hatching began, larvae were counted and assessed daily for swimming ability and gross physical deformities. Without exposing eggs to air, we changed the seawater in each jar every two days prior to hatching and daily after hatching began. All hatched larvae were collected, anesthetized with tricaine methanesulfonate, and preserved in 10% phosphate buffered formalin. Approximately the first and last 10% of larvae hatched from each female were preserved in separate bottles. Live larvae were preserved separately from dead larvae. After hatching was completed, remaining eggs were inspected; infertile eggs and dead embryos were counted.

A subset of preserved larvae was scored for yolk-sac edema, pericardial edema, and yolk volume. Ten females from the 1989 year class were randomly selected from each site, and 10 larvae per female were randomly selected from the central portion of hatched eggs for analysis. At Fish Bay, only five females from

[4] Brown, E. D. 1995. Alaska Department of Fish and Game. Commercial Fisheries Management and Development Division, PO Box 669, Cordova, AK 99574. Personal commun.

[5] Carls, M. G., D. M. Fremgen, J. E. Hose, S. W. Johnson, and S. D. Rice. In prep. Effects of incubating herring (*Clupea pallasi*) eggs in water contaminated with weathered crude oil. Auke Bay Laboratory, National Marine Fisheries Service, NOAA, 11305 Glacier Hwy., Juneau, AK 99801.

the 1989 year class were present; therefore the number of larvae analyzed per female was doubled. Sitka and St. Mathews Bay were excluded because of an insufficient number of females from the 1989 year class. Lateral views of larvae were displayed digitally, and specimens were rotated to align eyes in order to minimize variance. Yolk shapes were generally elliptical; major and minor axes were measured perpendicular to the body axis. Yolk volume was estimated from these linear measures according to the method of Hourston et al. (1984). Yolk-sac edema was indicated if the anterior margin of the yolk membrane was bounded by an area of clear fluid. Pericardial edema was scored if the pericardium was unusually large or convex ventrally.

Data processing and statistics

To assess the general health of parent fish, condition factor (K) was calculated for each female according to the method of Bagenal and Tesch (1978):

$$K = \frac{100(W)}{FL^b},$$

where W = somatic wet weight in g;
FL = fork length in cm; and
b = the value determined by site from length-weight regressions.

Gonad weight was substracted from body weight to avoid variation in spawning condition.

Times of hatching among sites, which were temperature dependent, were compared by using peak hatching times as the estimator. Peak hatching day was defined as the day the most larvae hatched from eggs of a given female; if two hatch peaks of equal magnitude occurred, the first peak was reported. Mean incubation temperature for eggs from each female was calculated by weighting mean water-bath temperatures by the number of eggs hatched daily. This method avoided possible under or over estimates of mean incubation temperature caused by early or late hatching of eggs as seasonal temperature increased.

Most observations were expressed as percentages. The denominator used to calculate percentages varied by response parameter (Table 1). Percentages of eggs fertile and initially dead were based on the total number of eggs counted near the beginning of the experiment. Percentages of eggs that hatched were based on the total number of hatched larvae plus the number of dead eggs determined at the endpoint. The number of hatched larvae was subdivided into number live, moribund, and dead. Hearts of moribund larvae were beating, but these larvae were incapable of movement. Accordingly, percent live was the number of living larvae (excluding moribund larvae) divided by the total number hatched. Swimming of live larvae was categorized as effective, ineffective, or incapable. Effective swimmers were active, frequented the water column, and avoided capture. Ineffective swimmers were generally more lethargic than effective swimmers and were more likely to be found on jar bottoms. Incapable swimmers were unable to swim in a straight line and were often capable only of spasmodic twitching. Swimming of moribund and dead larvae was, by definition, nonexistent; thus the number of live larvae was used as the denominator for swimming categories. Because larvae quickly became distorted after death, spinal aberrations were assessed only in live and moribund larvae. Percentage of spinal abnormalities, therefore, was the number of larvae with spinal aberrations divided by the sum of live and moribund larvae.

Table 1

Description of key response parameters used to evaluate reproductive impairment in Pacific herring collected from Prince William Sound and southeast Alaska. Herring were collected in 1995, artificially spawned, and reared in a laboratory until hatching. Moribund larvae were alive (heart beating) but incapable of swimming.

Parameter (%)	Description
Hatch	100 · (total number of eggs that hatched) /(total number of eggs that hatched + total number of dead eggs)
Live (viable)	100 · (total number of live larvae excluding moribund larvae) / (total number of eggs that hatched)
Effective swimmers	100 · (total number of effective swimmers) / (total number of live larvae excluding moribund larvae)
Spinal abnormalities	100 · (number of live + moribund larvae with spinal defects) / (total number of live + moribund larvae)

One-way analysis of variance (ANOVA) was used to examine differences among sites, among age classes, and between regions. Each reproductive parameter was tested separately by individual age class and for all age classes combined; percentage data were arc-sine transformed and corrected for small n as necessary (Snedecor and Cochran, 1980). To account for variance among sites, the F-test comparison between regions was:

$$F = \frac{MS_{between\ regions}}{MS_{among\ sites}}$$

where MS = mean square.

Somatic weight, FL, and K were analyzed similarly. Age-class responses within site were compared because in PWS different age classes were potentially exposed to varying levels of oil (Table 2). When the overall ANOVA was significant ($P \leq 0.05$), a priori multiple comparisons were used to identify which ages differed:

$$F = \frac{MS_{between\ age\ classes}}{MS_{error}}.$$

Maternal age was used as the standard in all age comparisons because ages frequently differed in the male and female crosses. Age-3 and age-4 herring were not exposed to oil at any life stage in PWS; therefore they were combined as site-specific controls. Few older age fish were captured; thus, ages ≥age 9 were combined and reported as 9+.

Because cold storage of adult fish (mean time of fish capture to mean spawning time) varied among sites (0.7–12.9 h), we also examined the possible effect of storage time on all reproductive parameters with storage time as a covariate in the ANOVA. Storage times up to 7 h did not significantly affect any of the key reproductive parameters ($P \geq 0.376$, except $P=0.084$ for % live larvae). We repeated the ANOVA for regional differences with storage times in the model as a covariate and restricted the analysis to include only those fish sampled within the same time period (≤7 h).

Scored yolk-sac edema was analyzed with the Kruskal-Wallis nonparametric test (SAS Institute Inc., 1989). Yolk-sac edema was also re-expressed as a percentage by female, arcsin-transformed, and analyzed by ANOVA. Yolk volume was analyzed by ANOVA.

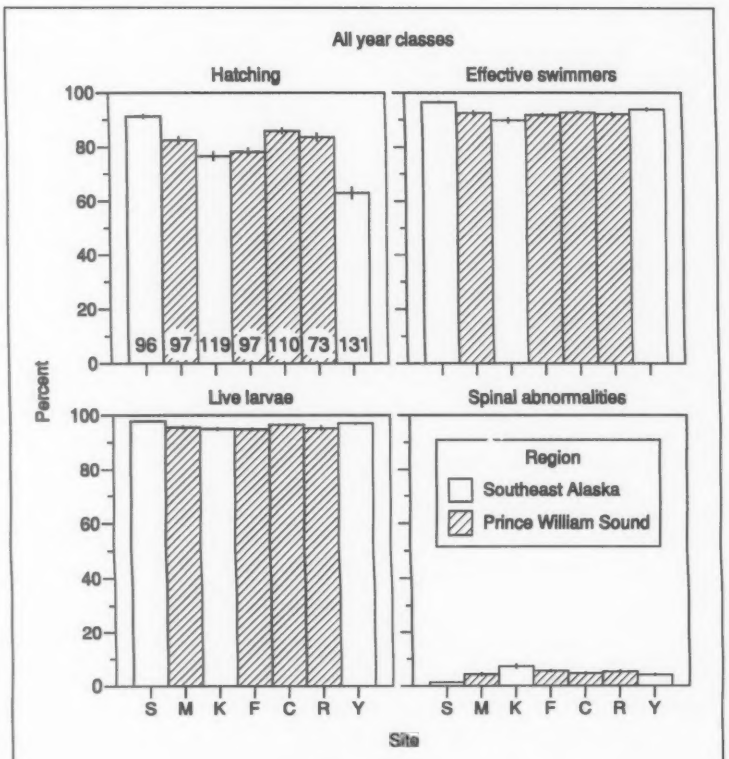

Figure 2

Mean (±SE) percent hatching, live, effective swimmers, and spinal abnormalities of larval Pacific herring by site and region in Alaska, 1995. S = Sitka, M = St. Mathews Bay, K = Ketchikan, F = Fish Bay, C = Port Chalmers, R = Rocky Bay, Y = Seymour Canal; sites in chronological order of spawning date. Sample size is shown in hatching graph. No significant differences existed between regions for any reproductive parameter ($P>0.50$).

Results

Regional comparison

Herring sampled from all sites appeared healthy and showed no obvious external signs of disease. For fish of the same age, there were no significant differences in FL ($P \geq 0.09$), weight ($P \geq 0.09$), or condition factor ($P \geq 0.41$) between regions. For herring in PWS, mean FL ranged from 196 to 260 mm and mean weight from 60.7 to 151.7 g, whereas in SE, mean FL ranged from 198 to 253 mm and mean weight from 65.1 to 140.4 g (Table 3).

For all age classes combined, reproductive success of herring did not differ significantly between regions ($P>0.50$); the best and worst responses generally occurred in SE, whereas PWS sites were intermediate (Fig. 2). Statistical power of these tests was high (≥0.99) and remained high for most analyses. Restricting the analysis to fish stored for ≤7 h did not alter the overall results; no significant ($P>0.39$) regional differences existed for any reproductive parameter. In SE, mean responses ranged from 63 to 91% for hatching success, 95 to 98% for live larvae, 90 to 96% for effective swimmers, and 1 to 7% for

Table 2

Age, year class, and possible oil exposure for Pacific herring collected in Prince William Sound, Alaska, in 1995. The *Exxon Valdez* oil spill occurred in March 1989.

Age	Year class	Possible oil exposure
3	1992	no direct oil exposure of any life stage
4	1991	no direct oil exposure of any life stage
5	1990	all life stages possibly exposed to residual oil
6	1989	all life stages likely exposed to oil
7	1988	juveniles at time of spill
8	1987	juveniles or immature at time of spill
9+	1986	mature—reproductive at time of spill

Table 3

Fork length (mm) and somatic weight (g) of mature female Pacific herring captured in southeast (SE) and Prince William Sound (PWS), Alaska, in spring 1995. Values are mean ($\bar{x}$) and ± standard error; sample size = n.

		Age (yr)								
		3	4	5	6	7	8	9	10	11
Fork length										
SE	$\bar{x}$	198	211	217	221	236	234	241	236	253
	±	1.9	2.9	2.0	1.2	1.3	3.5	8.4	3.5	7.7
	n	86	21	49	94	95	15	3	2	3
PWS	$\bar{x}$	196	219	225	236	242	260	259	259	260
	±	1.1	2.3	1.1	1.7	1.0	3.2	1.3	2.2	2.9
	n	81	18	65	25	149	10	16	7	13
Weight										
SE	$\bar{x}$	65.1	79.1	87.2	91.7	112.9	112.7	117.5	108.3	140.4
	±	1.8	3.2	2.1	1.7	1.9	5.1	4.6	6.4	14.7
	n	81	21	49	93	94	15	3	2	3
PWS	$\bar{x}$	60.7	90.3	95.0	107.4	121.0	149.0	147.8	148.9	151.7
	±	1.2	2.2	1.3	2.7	1.5	8.3	3.3	6.8	5.1
	n	80	18	65	25	149	10	16	7	13

spinal abnormalities. In PWS, mean responses ranged from 78 to 86% for hatching success, 95 to 96% for live larvae, 92 to 93% for effective swimmers, and 4 to 6% for spinal abnormalities. Among all sites, reproductive success was consistently best at Sitka (e.g. highest hatching success=91% and fewest spinal abnormalities=1%) and worst at Seymour Canal or Ketchikan (e.g. lowest hatching success=63% and most spinal abnormalities=7%) (Fig. 2). Of the sites in PWS, reproductive success was usually best at St. Mathews Bay or Port Chalmers (e.g. highest hatching success=86% and fewest spinal abnormalities=4%) and worst at Fish Bay (e.g. lowest hatching success=78% and most spinal abnormalities=6%) (Fig. 2). Similarly, when reproductive success was estimated for each age class individually, regional differences were not significant ($P>0.50$). This finding was true for all age comparisons—ages 3 to 9+. For example, age-6 (1989 year class) herring in PWS did not differ significantly from those in SE (Fig. 3). Among all sites where more than four age-6 fish were collected (excluding St. Mathews Bay and Sitka), hatching success ranged from 66% (Seymour Canal) to 91% (Port Chalmers), live larvae from 95% (Fish Bay) to 98% (Port Chalmers), effective swimmers from 93% (Rocky Bay) to 96% (Port Chalmers), and spinal abnormalities from 2% (Port Chalmers) to 6% (Fish Bay).

No significant regional differences were observed in progeny of the 1989 year class scored for physical condition. Only one larva of 500 had pericardial edema. Analyzed with the Kruskal-Wallis test, the site with the most yolk-sac edema (Port Chalmers) was significantly different from that with the least (Ketchikan), but there was no regional trend. Percentages of larvae with yolk-sac edema were low

(≤16%), and differences among sites and between regions were not significant ($P \geq 0.348$) (Fig. 4).

Yolk volume in larvae from the 1989 year class did not differ significantly ($P=0.486$) between regions but may have been related to incubation temperature. The largest and smallest mean yolk volumes were observed in PWS but closely overlapped those in SE (Fig. 4). Although scatter was high ($r^2=0.13$), yolk volumes declined significantly ($P<0.001$) as temperature increased. It is possible, however, that site differences and incubation temperature were confounding factors.

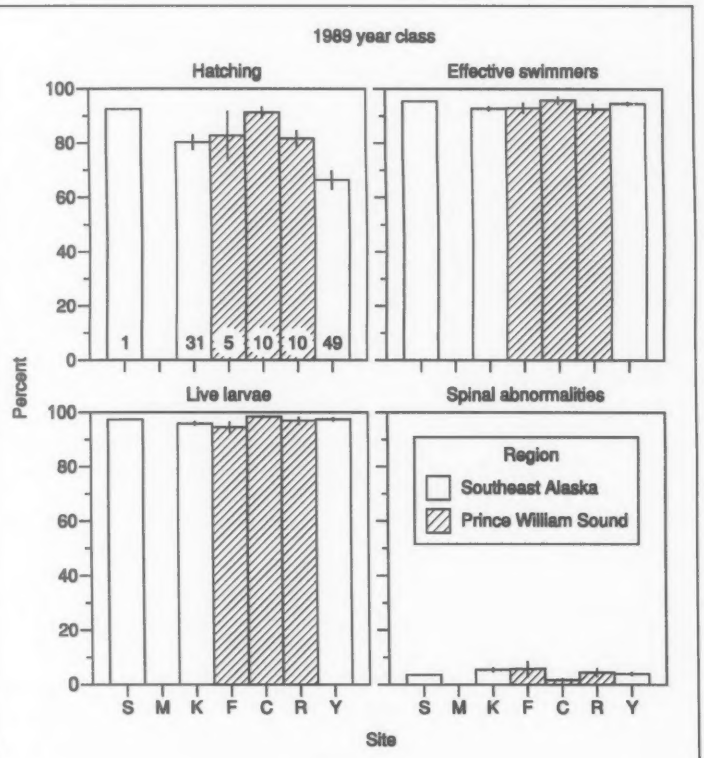

Figure 3

For the 1989 year class, mean (±SE) percent hatching, live, effective swimmers, and spinal abnormalities of larval Pacific herring by site and region in Alaska, 1995. The 1989 year class, sampled in Prince William Sound in 1995, was more likely exposed to oil as eggs or larvae than were other year classes. S = Sitka, M = St. Mathews Bay, K = Ketchikan, F = Fish Bay, C = Port Chalmers, R = Rocky Bay, Y = Seymour Canal. Sample size is shown in hatching graph. Progeny of the 1989 year class did not differ significantly between regions for any reproductive parameter ($P>0.50$).

Comparison among age classes within sites

Reproductive success differed significantly among some age classes at Sitka, Ketchikan, Port Chalmers, and Rocky Bay but not among age classes at St. Mathews Bay, Fish Bay, and Seymour Canal (Figs. 5–8). The few significant differences we observed were highly variable, inconsistent among sites, and no pattern existed for the 1989 year class. For example, at Rocky Bay, age-3 and age-4 fish had a significantly lower percentage of live larvae than age-5, age-6, and age-7 fish (Fig. 6), whereas at Sitka, age-3 and age-4 fish had a significantly higher percentage of effective swimmers and a significantly lower percentage of spinal abnormalities than age-7 fish (Figs. 7 and 8).

Other parameters

Hatching times decreased steadily with increasing incubation temperature (Fig. 9). For Sitka, the first site sampled, peak hatching occurred about 33 d after start of incubation at a mean temperature of about 4.5°C, whereas at Seymour Canal, the last site sampled, peak hatching occurred about 26 d after start of incubation at a mean temperature of about 6.0°C.

Fertility did not differ significantly ($P>0.50$) between regions for all ages combined or when the comparison was restricted to fish of the same age. For all ages combined, fertility in SE ranged from 80% at Seymour Canal to 96% at Sitka; in PWS, fertility ranged from 88% at Fish Bay to 94% at St. Mathews Bay.

Discussion

Six years after the spill, reproductive impairment was not detected in PWS herring. This conclusion was reached by comparing reproductive success of fish collected in PWS and SE and among age classes within specific sites. Specifically, hatching success, larval viability, and fertility did not differ significantly between PWS and SE, including response of the 1989 year class. In fact, discrimination of responses between regions was not possible because the best and worst responses were usually found in

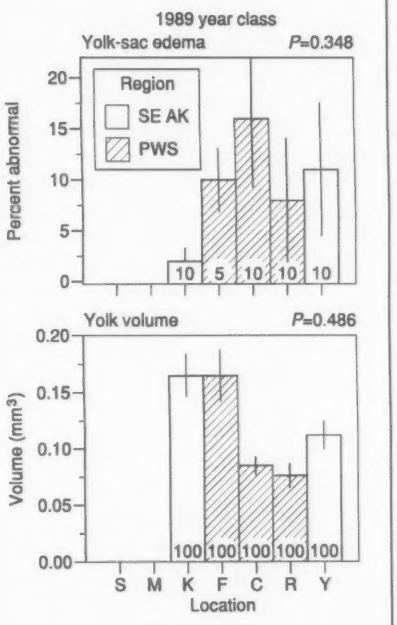

Figure 4

For the 1989 year class, mean (±SE) percent yolk-sac abnormalities (edema) and yolk volume for larval Pacific herring by site and region in Alaska, 1995. Sample size is shown in each bar. S = Sitka, M = St. Mathews Bay, K= Ketchikan, F = Fish Bay, C = Port Chalmers, R = Rocky Bay, Y = Seymour Canal. No significant differences existed between regions for either parameter ($P \geq 0.348$).

one region (SE). Therefore, the chances of detecting any oil-related effects against the natural background variation were negligible when herring were compared between regions. Although responses among some age classes within Port Chalmers and Rocky Bay were occasionally significant, these differences were highly variable, did not indicate reproductive impairment of the 1989 year class, and were inconsistent between sites.

Of the four key reproductive parameters we examined, spinal defects were particularly important because exposure of herring eggs to oil frequently causes spinal defects (Linden, 1978; Kocan et al., 1987; Rice et al., 1987; Pearson et al.[6]), that could result in reduced swimming ability and long-term survival. Spinal defects, however, can also occur naturally as a result of other environmental factors. In our study, herring from an uncontaminated site, Ketchikan, had the highest percentage of spinal defects (7%). Ketchikan samples were collected at least 40 km from any urban area, and it is unlikely that these fish were exposed to industrial or other urban pollutants. Whether the incidence of spinal defects at Ketchikan was just random noise or a response to some underlying environmental factor is impossible to determine, but it is evidence that similar results could occur in PWS without implicating oil as a cause. In fact, a 10% incidence of gross abnormalities was observed in PWS herring 23 years prior to the spill (Smith and Cameron, 1979).

Reproductive success of herring in PWS was consistently better in 1995 than that reported in earlier studies. For example, we observed a mean hatching success of 78–86% compared with 53% in 1976 (Smith and Cameron, 1979), 62%[7] in 1989 (McGurk et al.[8]), 85% in 1990 (McGurk et al.[9]), 59–79% in 1991 (Kocan et al., 1996a), and 19–56% in 1992 (Kocan et al., 1996b). The viable hatching[10] that we observed in PWS (79%) also exceeded previously reported percentages; 53%[11] in 1989 (McGurk et al.[8]), 57% in 1990 (McGurk et al.[9]), 35–37%[12] in 1991 (Kocan et al., 1996a), and 13–33%[12] in 1992 (Kocan et al., 1996b). Incidence of spinal abnormalities in PWS was about 5% in our study compared with 7% in 1989 (McGurk

[6] Pearson, W. H., D. L. Woodruff, S. L. Kiesser, G. W. Fellingham, and R. A. Elston. 1985. Oil effects on spawning behavior and reproduction in Pacific herring (*Clupea harengus pallasi*). Final Report OF-1742 to American Petroleum Inst., Battelle Marine Res. Lab., Sequim, WA, 108 p. [API publication 4412.]

[7] To avoid desiccation effects, and because egg survival was significantly less in the +1.5-m collections in the McGurk et al.[8] data set, these data were not included in this comparison. Estimated egg survival was 59% when the +1.5-m data were included.

[8] McGurk, M., D. Warburton, T. Parker, and M. Litke. 1990. Early life history of Pacific herring: 1989 Prince William Sound herring egg incubation experiment. Final report, contract number 50ABNC-7-00141, Triton Environmental Consultants LTD., No. 120-13511 Commerce Parkway, Richmond, British Columbia, Canada V6V 2L1.

[9] McGurk, M., T. Watson, D. Tesch, B. Mattock, and S. Northrup. 1991. Viable hatch of Pacific herring eggs from Prince William Sound and Sitka Sound, Alaska, in 1990. Report number 2060/WP 4269, Triton Environmental Consultants LTD., No. 120-13511 Commerce Parkway, Richmond, British Columbia, Canada V6V 2L1.

[10] To conform with McGurk et al.[8,9], % viable hatch was defined as 100 [(no. live larvae – no. abnormal larvae)/(no. hatched eggs)] × (no. eggs hatched/no. eggs total). The value defined by Kocan et al. (1996, a and b) as % viable larvae is nearly synonymous with % viable hatch. Our % live larvae (Table 1) included abnormal larvae, but McGurk et al.[8,9] excluded abnormal larvae in their definition of % viable larvae (% viable = 100 (no. live larvae – no. abnormal larvae)/no. hatched).

[11] As previously, +1.5-m data were not included; estimated % viable hatch was 50% when these data were included.

[12] Percent viable larvae values reported by Kocan et al. (1996, a and b) should be increased by 2% to approximate percent viable hatch.

et al.[8]). Although procedural differences between earlier studies and ours may partially account for differences in assessment of reproductive success, the responses we observed in 1995 were consistently the best.

To interpret the effects of the spill on herring in PWS, it is necessary to understand the life stage exposed and the magnitude and duration of exposure. Which life stages were impacted, and to what extent, however, is largely a matter of conjecture. Adult fish may have encountered oil before, during, or after spawning, but determining what percentage of the population was significantly impacted is impossible. Metabolites of aromatic hydrocarbons were detected in adult herring (Haynes et al.[13]), but sample sizes were very low. Nematode prevalence in adult body cavities differed significantly between contaminated and uncontaminated areas (Moles et al., 1993), also indicating adult exposure. The duration and magnitude of oil exposure of herring eggs and larvae is also unknown. After hatching, herring larvae from both contaminated and uncontaminated sites may have been exposed to oil as they passively traversed the spill trajectory. For example, some of the largest concentrations of larvae in June were found in the southwest portion of PWS, well within the oil trajectory (Norcross et al., 1996). By inference, juvenile herring occupying the same nearshore habitat used by juvenile salmonids may have also been exposed to oil: such exposure was documented in juvenile pink and chum salmon (Carls et al., 1996).

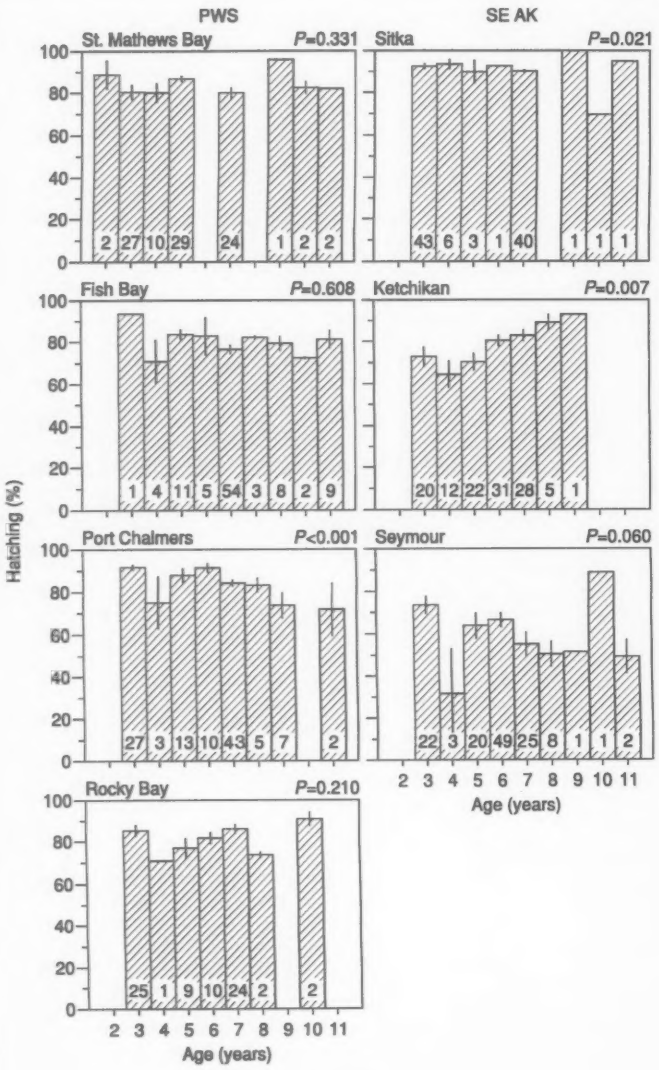

Figure 5

Mean (±SE) percent hatching of larval Pacific herring by female parent age, site, and region in Alaska, 1995. Sample size is shown in each bar. Overall *P*-value from ANOVA is listed above each graph. Significant differences were Ketchikan, ages 3 and 4 < age 6, 7, and 8 ($P \leq 0.015$); Port Chalmers, ages 3 and 4 > age 9+ ($P = 0.050$).

Response of wild herring to an oil spill can be partially inferred from laboratory studies. For example, exposure of mature herring to hydrocarbons in the laboratory did not cause discernible damage in progeny, including fertility, viability, and larval swimming, physical, and genetic abnormalities (Rice et al., 1987; Carls et al.[14]). In contrast, the early life

[13] Haynes, E., T. Rutecki, M. Murphy, and D. Urban. 1995. Impacts of the *Exxon Valdez* oil spill on bottomfish and shellfish in Prince William Sound, *Exxon Valdez* oil spill state/federal natural resource damage assessment final report (fin/shellfish study no. 18). Auke Bay Laboratory, National Marine Fisheries Service, 11305 Glacier Hwy., Juneau, AK 99801.

[14] Carls, M. G., D. M. Fremgen, J. E. Hose, D. Love, and R. E. Thomas. 1995. The impact of exposure of adult pre-spawn herring (*Clupea harengus pallasi*) on subsequent progeny. Chapter 2 *in* Carls et al., *Exxon Valdez* oil spill report, restoration project 94166, annual report; the impact of exposure of adult pre-spawn herring (*Clupea harengus pallasi*) on subsequent progeny, p. 29–49. Auke Bay Laboratory, NMFS, NOAA, 11305 Glacier Hwy., Juneau, AK 99801.

stages of herring are more susceptible to the effects of oil according to laboratory (Linden, 1978; Pearson et al., 1985; Carls, 1987; Kocan et al., 1987; Rice et al., 1987) and field studies (Brown et al., 1996a; Norcross et al., 1996). Abnormal larvae have poor survival potential (Kocan et al., 1996a), and thus the exposure of eggs and larvae to oil in PWS may have resulted in increased mortality. Furthermore, the same oil concentrations that caused significant genetic damage also caused significant physical damage in developing embryos (Carls et al.[5]); thus early death would likely preclude recruitment of genetically damaged individuals to spawning populations.

Although genetic damage was detected in larvae collected in the oil-contaminated areas of PWS in 1989 (Hose et al., 1996; Brown et al., 1996a), we did not inspect larvae for genetic damage. Concomitant laboratory measurements of larvae that had been artificially contaminated indicated that genetic response was not a more sensitive measure of oil exposure than the parameters we examined (Carls et al.[5]). In addition, artificial exposure of prespawning adults to relatively high oil concentrations (58 ppb, initial PAH) did not cause genetic defects in artificially spawned progeny (Carls et al.[14]). Other defects observed in larvae from PWS in 1989 included physical damage, assessed by scored indices (Hose et al., 1996). Carls et al.[5] observed that two of these indices, pericardial edema and finfold condition, were more sensitive to oil damage than was the genetic response. Because we did not detect significant pericardial abnormalities in larvae from PWS six years after the spill, it is likely that the genetic condition of these larvae has not been adversely affected.

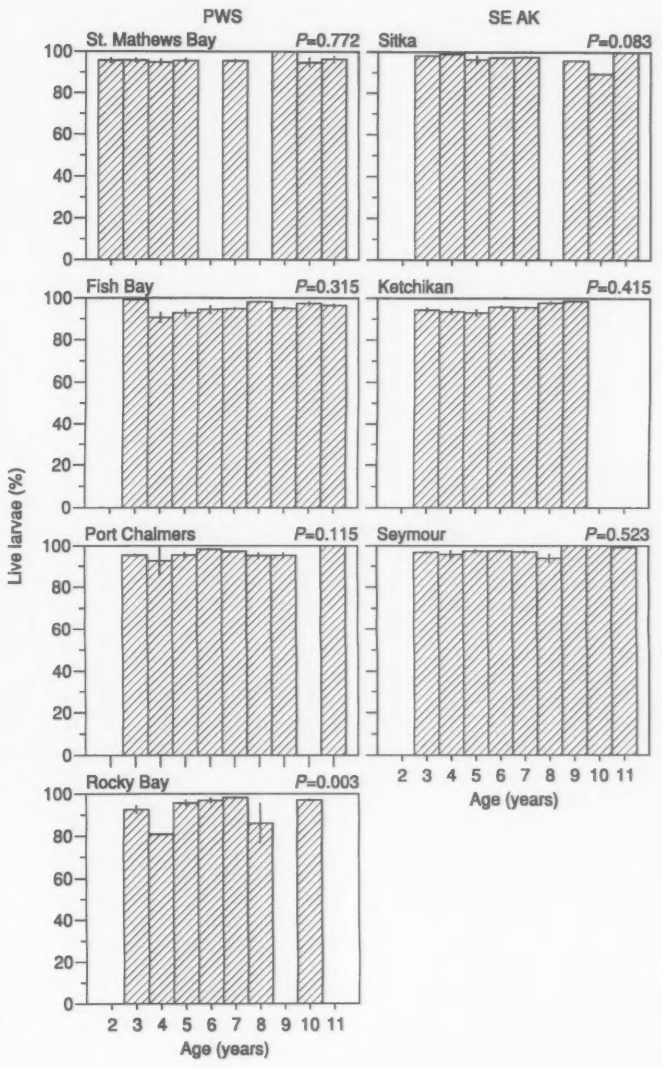

Figure 6

Mean (±SE) percent live larvae of Pacific herring by female parent age, site, and region in Alaska, 1995. Sample sizes are indicated in Figure 5. Overall *P*-value from ANOVA is listed above each graph. Significant differences were Rocky Bay, ages 3 and 4 < age 5, 6, and 7 ($P \leq 0.047$).

The failure of the 1989 year class of herring in PWS to recruit to the spawning population may have been partly attributable to the spill, but it is impossible to separate oil effects from other natural factors. At the sites we sampled in PWS, the 1989 year class usually represented <4.0% of the spawning population (ADF&G[15]). Larval survival in PWS was reduced an estimated 52% in 1989 as a result of the spill (Brown et al., 1996a); such loss supports inferences of poor survival that are based on laboratory obser-

[15] ADF&G (Alaska Department of Fish and Game). 1995. Herring test fishery data. Commercial Fisheries Management and Development Division, PO Box 669, Cordova, AK 99574.

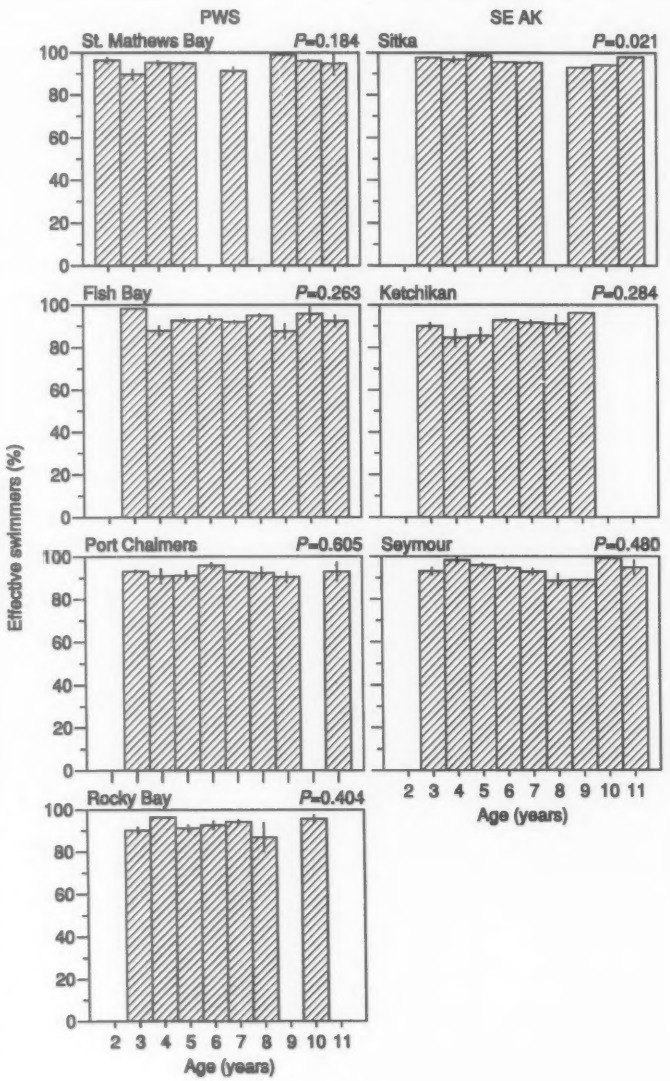

Figure 7

Mean (±SE) percent effective swimmers of larval Pacific herring by female parent age, site, and region in Alaska, 1995. Sample sizes are indicated in Figure 5. Overall *P*-value from ANOVA is listed above each graph. Significant differences were Sitka, ages 3 and 4 > age 7 (P=0.011).

vation. Natural environmental conditions, however, can also cause a high degree of variability in herring recruitment (Stevenson, 1962; Anthony and Fogarty, 1985). For example, the 1989 year class at Sitka also represented a small proportion of the spawning population in 1995 (<2%; ADF&G[16]); therefore factors other than oil are important determinants of cohort size.

Whether or not herring in PWS were ever reproductively impaired by the EVOS is unknown, but the time lapse between the spill and our study probably precluded any detection of reproductive impairment.

[16] ADF&G (Alaska Department of Fish and Game). 1995. Herring test fishery data. Commercial Fisheries Management and Development Division, 304 Lake St., Room 103, Sitka, AK 99835.

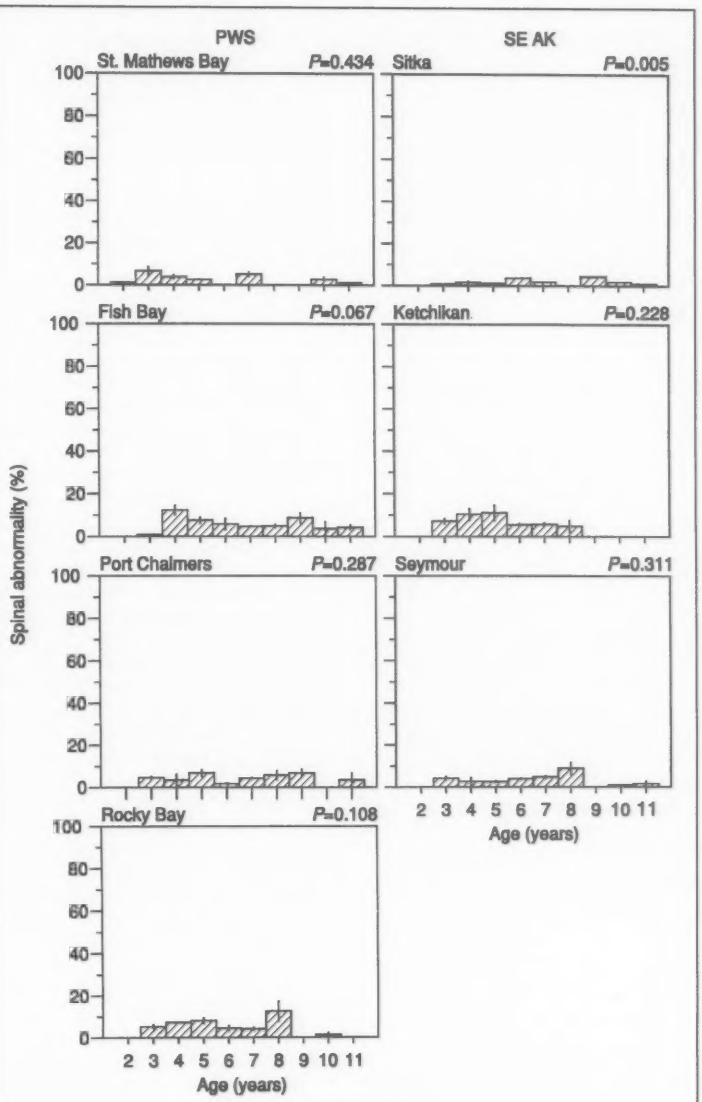

Figure 8

Mean (±SE) percent spinal abnormalities of larval Pacific herring by female parent age, site, and region in Alaska, 1995. Sample sizes are indicated in Figure 5. Overall *P*-value from ANOVA is listed above each graph. Significant differences were Sitka, ages 3 and 4 < age 7 (P=0.024).

Measurable effects likely declined most rapidly during the first year as the most adversely affected individuals died. Although oil-related abnormalities were observed in larvae immediately following the spill, both developmental and genetic damage progressively decreased with time (Brown et al., 1996a) and were undetectable in 1990 and 1991 (Hose et al., 1996). The extent of spawning-site fidelity in herring is poorly understood, but unaffected individuals from other geographic areas have probably joined remaining, less affected spawners, diluting possible residual effects. The disease epidemic observed in PWS in 1993 (Meyers et al., 1994) may have removed additional marginal spill survivors. Thus, it is not particularly surprising that reproductive impairment was not detected in 1995.

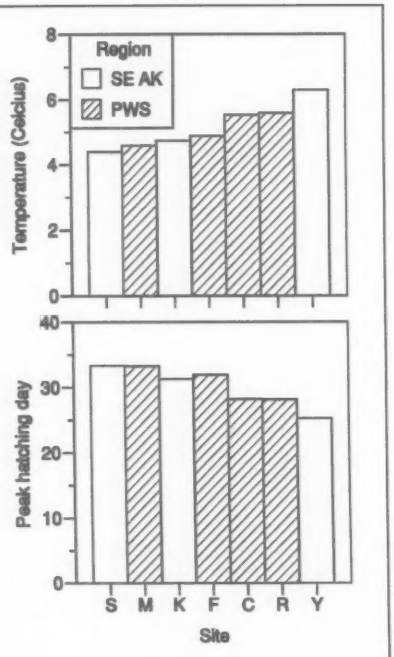

Figure 9

Peak hatching day and mean (±SE) incubation temperature (°C) for eggs spawned from mature Pacific herring by site and region in Alaska, 1995. S = Sitka, M = St. Mathews Bay, K = Ketchikan, F = Fish Bay, C = Port Chalmers, R = Rocky Bay, Y = Seymour Canal; sites are in chronological order of spawning date.

Understanding the long-term implications of exposure of Pacific herring to oil in PWS was the principal objective of this research. Regardless of the life stage of herring and the likelihood of possible oil exposure, herring we sampled in PWS in 1995 appeared to be reproductively fit and similar to herring in SE. Although herring stocks are still depressed in PWS, factors other than reproductive impairment are probably limiting recovery.

Acknowledgments

We thank John Campbell, Jamison Clark, Mary Drew, Dan Fremgen, Chris Hanson, Dave Love, Xiaohong Luan, Nathan Magaret, Joshua Millstein, Catherine Pohl, Jeff Regelin, June Sage, Michele Sleeter, and Justin Stekoll for technical laboratory assistance. We also thank the Alaska Department of Fish & Game Commercial Fisheries Division in Sitka, Ketchikan, Juneau, and Cordova for help in collecting herring and for providing laboratory space. The research described in this paper was supported by the *Exxon Valdez* Oil Spill Trustee Council. The findings and conclusions presented by the authors, however, are their own and do not necessarily reflect the view or position of the Trustee Council.

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Abstract.—We examine the population to population variability of intrinsic rate of natural increase, r_m, of Atlantic cod, *Gadus morhua*. The intrinsic rate of increase is positively related to temperature, contrary to the expectation that r_m might increase as the high and low temperature limits of habitability for cod are approached. For the parameter regime considered, r_m has a simple dependence on age-at-maturity and the number of replacements each spawner can produce at low population densities ($\tilde{\alpha}$). It is shown that $\tilde{\alpha}$ has no significant temperature dependence, and thus the covariation of r_m and temperature arises from the influence of temperature on age-at-maturity. We demonstrate that our estimates of r_m are robust and thus may be of use in estimating the recovery time of depleted populations.

Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*

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Perhaps the most fundamental of all ecological parameters is the intrinsic rate of natural increase, r_m (Cole, 1954; Pimm, 1991). High r_m will be selected for in populations that experience frequent excursions to low density (Charlesworth, 1994). Populations subjected to strong environmental variability should evolve toward high r_m (MacArthur and Wilson, 1967), which will impart resilience to the population. However, allometric (cross species) comparisons (Fenchel, 1974; Hennemann. 1983; Charnov, 1993) suggest that r_m chiefly depends on metabolic rate or somatic growth rate. Perhaps, the influence of environmental variability on r_m can be more readily discerned in cross population comparisons for a single species. In this paper we examine 20 populations of Atlantic cod, *Gadus morhua*, to determine their maximum growth rates. We also discuss how these estimates help predict the recovery times of severely overfished populations.

Atlantic cod lends itself to a study of this nature because there is a wealth of good quality biological data collected for stock management purposes. Moreover, these cod populations occupy a broad span of latitudes, including regions that are thought to represent the northern and southern limits of habitability for cod, and there is evidence that population variability increases as these extremes are approached (Myers, 1991). The increase in population variability at the limits of the range of cod could impose constraints on r_m that would mask the simple dependence of r_m on metabolic rate or somatic growth rate apparent in cross species comparisons. In fact, we will show, in what we believe is an unanticipated result, that even for a within-species comparison, there is strong coupling between r_m and metabolic rate or somatic growth rate (as represented by age at maturity or temperature). Our results have implications for the recovery rates of a number of

recently collapsed Atlantic cod populations (Hutchings and Myers, 1994).

Methods

Model

For fish populations, reproduction is generally expressed as recruitment, the number of juvenile fish reaching, in a given year, the age of vulnerability to fishing gear. Thus, the reproduction curve (Royama, 1993) for fish is displayed as a spawner-recruitment curve (Ricker, 1954), and r_m must be derived from the slope of this curve near the origin (low population). This derivation will be presented immediately following a brief discussion of the standard population-recruitment curves.

Juvenile fish become vulnerable to fishing gear, that is, they recruit at an age designated as j'. We consider the Ricker spawner-recruitment model which describes the number of recruits at age j' in year $t+j'$, $N\ t+j', j'$, resulting from a spawning stock biomass (SSB) of S_t. We follow the usual convention in fisheries science of assuming that the number of eggs produced is proportional to the biomass of spawners.

The Ricker model has the form

$$E(N_{t+j',j'}) = \alpha S_t e^{-\beta S_t}, \tag{1}$$

where α = the slope at the origin (measured perhaps in recruits per kilogram of spawners). Density-dependent mortality is assumed to be the product of β multiplied by the spawning biomass (S_t).

For the forthcoming calculations the slope at origin, α, must be standardized. First consider

$$\hat{\alpha} = \alpha \cdot \mathrm{SPR}_{F=0},$$

where $SPR_{F=0}$ is the spawning biomass resulting from each recruit (perhaps in units of kg of spawning fish per recruit) in the limit of no fishing mortality (F=0). This quantity, $\hat{\alpha}$, represents, on a lifetime basis, the number of recruits per recruit at very low spawner abundance or, equivalently, the number of spawners produced per spawner (assuming that there is constant survival from recruit to spawner).

The quantity, $\tilde{\alpha}$, required for our calculations is the number of spawners produced by each spawner per year (after a lag of a years, where a is age-at-maturity).

If adult survival is p_s then $\tilde{\alpha} = \Sigma_j\, p_s^{\,j}\hat{\alpha}$, or summing the geometric series

$$\tilde{\alpha} = \hat{\alpha}(1-p_s) = \alpha \cdot \mathrm{SPR}_{F=0}(1-p_s). \tag{2}$$

If the annual survival fraction for spawners was zero, the population of spawners, N_t, would obey the following equation:

$$N_{t+a} = \tilde{\alpha} N_t. \tag{3}$$

Equation 3 has the solution $N_{t=na} = \tilde{\alpha}^n N_0$, where N_0 is the number of spawners at t = 0. It follows that the natural growth rate, per annum, of the population is

$$r_m = (1/a)\log\tilde{\alpha}, \tag{4}$$

for the limit of small p_s. The analogous result for the case of overlapping generations is derived below.

When adult survival in not zero ($p_s \neq 0$), one has an age-structured spawning population, and r_m cannot be derived in the simple manner presented above. Rather, one must solve the Euler-Lotka equation (Charlesworth, 1994) to obtain r_m in this situation.

The Euler-Lotka equation is

$$\sum_j l_j m_j e^{-r_m j} = 1, \tag{5}$$

where l_j = the fraction of animals surviving to age j; and
m_j = the number of offspring per animal produced at age j.

We now assume that $m_j = m_0$ for fish of age a and older, and also, for $j \geq a$, $l_j = l_a\, p_s^{\,j-a}$, where l_a is the fraction of juveniles that survive from age zero to age a, and, again, p_s is the annual survival fraction of spawners. It follows from Equation 5 that

$$l_a m_0 \sum_{j=a}^{j=\infty} p_s^{\,j-a} e^{-r_m j} = 1. \tag{6}$$

A little manipulation, and the summing of a geometric series, allows Equation 6 to be written as

$$\frac{l_a m_0 e^{-r_m a}}{1 - p_s e^{-r_m}} = 1. \tag{7}$$

Since m_0 is the number of age-zero fish produced by each spawner, and since l_a is the fraction of age-zero fish surviving through the juvenile stage to maturity, it follows that $m_0 l_a = \tilde{\alpha}$, and thus Equation 7 can be expressed as

$$(e^{r_m})^a - p_s(e^{r_m})^{a-1} - \tilde{\alpha} = 0. \tag{8}$$

We have bracketed the e^{r_m} m term to emphasize that Equation 8 is a simple algebraic equation for $\chi = e^{r_m}$. Note that in the limit $p_s = 0$, we recover Equation 4 from Equation 8. Equation 8 is very similar to Equation 1 of Goodman (1984), amounting to a translation into parameters available for fish populations. Equation 8 may also be obtained as the low density limit of the simplified age-structured model of Clark (1976), as modified by Mertz and Myers (1996).

It is clear for a moderately large slope at the origin ($\tilde{\alpha}$) that age of maturity (a) is the most important factor in determining r_m (Fig. 1). The solid line in Figure 1 shows, for reference, the case $p_s = 0$, for which r_m may be calculated from Equation 4. The three broken lines in Figure 1 represent $p_s = 0.7$, 0.8, 0.9, a range that should encompass all North Atlantic cod stocks (see next section). For this range, survival after reproduction (p_s) has only a minor effect on r_m.

Data sources and treatment

The data we used are estimates obtained from assessments compiled by Myers et al. (1995b). Population numbers and fishing mortality were estimated by using sequential population analysis (SPA) of commercial catch-at-age data for most marine populations. Sequential population analysis techniques include virtual population analysis (VPA), cohort analysis, and related methods that reconstruct population size from catch-at-age data (see Hilborn and Walters, 1992) chapters 10 and 11, for description of the methods used to reconstruct the population history). Briefly, the commercial catch-at-age is combined with estimates from research surveys and commercial catch rates to estimate numbers-at-age in the final year and to reconstruct previous numbers-at-age under the assumption that commercial catch-at-age is known without error and that natural mortality-at- age is known and constant.

The population boundaries in the North Atlantic generally follow those of the Northwest Atlantic Fisheries Organization (NAFO) or the International Council for the Exploration of the Sea (ICES) (Fig. 2). Many populations cover more than one NAFO or ICES unit area, e.g. the cod population off Labrador and Northeast Newfoundland, known as "northern" cod, inhabits three NAFO divisions (2J, 3K, and 3L) and is designated as 2J3KL cod. There are three minor populations that are not included in the comparative analysis: Flemish Cap, Gulf of Maine, and the English Channel. There are no reliable catch data for the Flemish Cap population (NAFO 3M) or the English Channel population (ICES VIId), and the

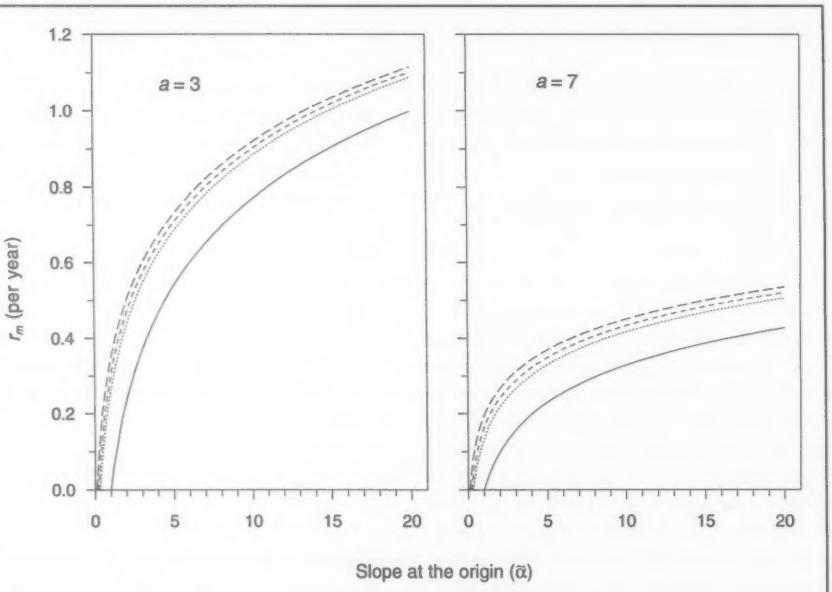

Figure 1

Rate of population growth (r_m) as a function of slope at the origin ($\tilde{\alpha}$) at minimum population size, age of maturity (a), and adult survival rates $p_s = 0$ (solid line), $p_s = 0.7$ (dotted line), $p_s = 0.8$ (short-dashed line), and $p_s = 0.9$ (long-dashed line)

time series of data for the Gulf of Maine (NAFO 5Y) is not included in the comparative analysis because the time series is too short (less than 10 years) (Myers et al., 1995b).

Maturity and weight-at-age were estimated from research surveys carried out for each population. Typically hundreds of fish are measured from a stratified random or systematic design each year. Adult natural mortality (M) has been investigated by a variety of methods; for each of the 20 populations, the value of M=0.2 was accepted by the researchers studying each population. This natural mortality corresponds to adult survival of $p_s = e^{-M} \approx 0.8$ (which will be our working value). The uniformity (across populations) of acceptable values for p_s suggests that one can safely assume that the true p_s lies in the range 0.7 to 0.9, as shown in Figure 1.

Bottom temperature was estimated by Brander (1994) for all the populations except the Baltic populations. We used data in Dickson et. al. (1992) to make estimates for the Baltic populations. We estimated independent temperatures for the Northwest Atlantic from deYoung et. al. (1994). These changes were small (less than 2°C) and did not have an important effect on our findings.

Estimation

The slope at the origin, $\tilde{\alpha}$, and other parameters of the Ricker model were fitted by using maximum-likelihood estimation and by assuming lognormal variability in the residuals (Hilborn and Walters, 1992); the assumption of gamma variability in model residuals resulted in only minor changes in the esti-

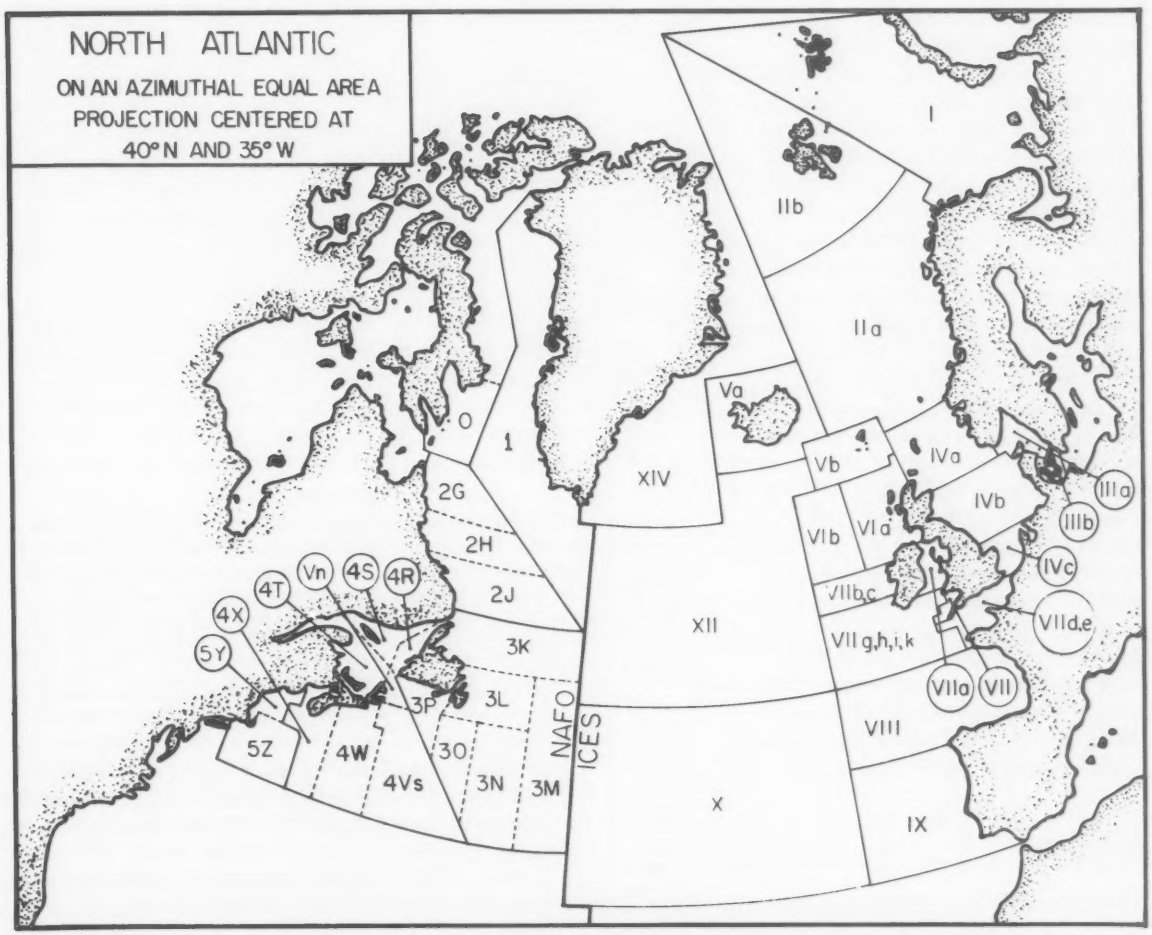

Figure 2

Map of the North Atlantic showing the regions used to define fish populations for fisheries management.

mated parameters (Myers et al., 1995b). Difficulties in estimating density-dependent model parameters are well known for insect and bird populations (Holyoak, 1993; Wolda and Dennis, 1993) and have been extensivly studied for exploited fish populations (Hilborn and Walters, 1992). The most important source of statistical bias for exploited fish populations is the nonindependence of spawners and recruitment, i.e. large recruitment usually leads to large spawner abundance (Walters, 1985). Bias in the parameter estimates of the spawner recruit function has been extensively studied with simulations for cod populations by Myers and Barrowman (1995) who found minimal bias in the estimates of the α parameter.

The slope at the origin can be well estimated for cod populations, in spite of the large variability in recruitment, because each population has been reduced to very low levels by overexploitation (Myers et al., 1994). Furthermore, there is no evidence that mortality increases at low population size, i.e. depensation or the Allee effect, that would invalidate the assumption of our spawner recruitment model (Myers et al., 1995).

The disadvantage of using the Ricker model, or any other parametric spawner recruitment model, is that the slope at the origin is influenced by observations far from the origin. We investigated an alternative approach: we regressed recruitment versus spawner biomass with only six observations with the lowest spawner biomass, forcing the regression line through the origin. This simple procedure should be reasonable because all the populations have been reduced to very low levels.

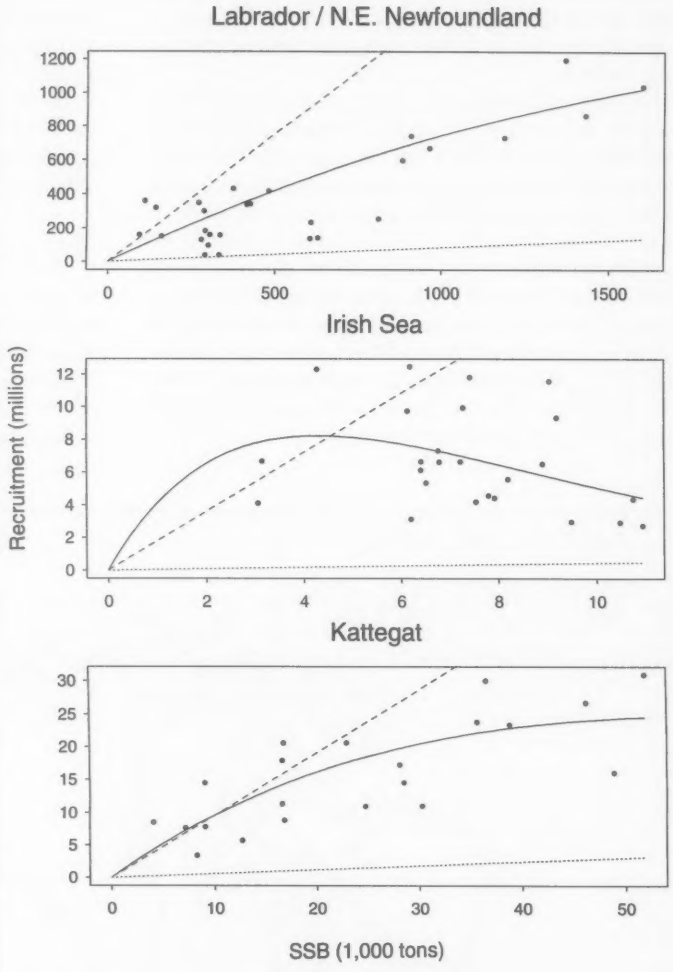

Figure 3

Recruitment versus spawning stock biomass (SSB) for the three representative cod populations. The solid line is the maximum likelihood estimate of the mean for Ricker spawner-recruitment functions under the assumption that the probability distribution for any SSB is given by a lognormal distribution. The dashed line is the median slope at the origin estimated from the six points with the lowest SSB. The straight dotted line is the replacement line with no fishing mortality.

Results

The Ricker model estimates of the slope at the origin and of the population growth rate were estimated for the 20 spawner recruit data sets (Table 1; Fig. 3). The slope at the origin, $\tilde{\alpha}$, did not vary enormously among populations (Fig. 4). There is one population, Irish Sea, for which the $\tilde{\alpha}$ is much larger; we believe that this large $\tilde{\alpha}$ is an overestimate (this will be discussed later).

It is evident that r_m strongly covaries with temperature (Fig. 5; Table 2). It is also clear that this behavior does not arise from any dependence of $\tilde{\alpha}$ on temperature, because $\tilde{\alpha}$ is not correlated with temperature (Fig. 5; Table 2). There is a strong de-

Table 1

Estimates of rate of population growth (r_m), slope at the origin ($\tilde{\alpha}$) estimated from the Ricker model, age of maturity (a), bottom temperature, and NAFO/ICES management units for 20 cod populations in the North Atlantic.

ID no.	Stock location	NAFO/ICES management unit	r_m	$\tilde{\alpha}$	a	Temperature
1	West Greenland	1	0.23	2.4	6	1.75
2	Labrador/N.E. Newfoundland	2J3KL	0.17	2.3	7	0.00
3	S. Grand Bank	3NO	0.27	3.5	6	1.75
4	N. Gulf of St. Lawrence	3Pn4RS	0.20	3.0	7	1.00
5	St. Pierre Bank	3Ps	0.31	4.6	6	2.50
6	S. Gulf of St. Lawrence	4TVn	0.15	1.9	7	1.75
7	E. Scotian Shelf	4VsW	0.36	9.8	6	3.75
8	S.W. Scotian Shelf	4X	0.36	2.5	3.5	6.75
9	Georges Bank	5Z	0.60	2.2	2	8.00
10	S.E. Baltic	22–24	0.74	8.4	3	7.00
11	Central Baltic	25–32	0.53	3.1	3	5.00
12	Celtic Sea	VIIg,f	0.62	5.3	3	11.00
13	Faroe Plateau	Vb	0.44	4.2	4	7.40
14	Iceland	Va	0.24	4.3	7	5.80
15	Irish Sea	VIIa	1.03	23.1	3	10.00
16	Kattegat	South IIIa	0.53	3.8	3	6.50
17	Barents Sea	I	0.26	6.6	7.5	4.00
18	North Sea	IV	0.56	9.0	4	8.60
19	Skagerrak	North IIIa	0.82	11.2	3	6.50
20	West of Scotland	VIa	0.80	6.4	2.5	10.00

pendence of r_m on age-at-maturity, but there is no corresponding significant relation between $\tilde{\alpha}$ and age-at-maturity (Fig. 6). Consistency demands that there be a relation between age-at-maturity and temperature, and, indeed, Table 2 and Figure 7 show that there is a significant correlation between these two variables.

We repeated the above analysis with $\tilde{\alpha}$ calculated at the median slope of the six observations with the lowest spawner abundance. The estimates calculated with this robust procedure were generally comparable with those estimated from the Ricker model, although the Ricker values were generally higher (Fig. 8). The larger discrepancies in the two methods occurred for the populations in which there were low estimates of recruitment at the largest population sizes, e.g. Irish Sea cod (Fig. 3). These points, although they are farthest from the origin, resulted in a higher estimate of the slope at the origin because the Ricker model assumes a linear relation between egg-to-recruit mortality and SSB.

We repeated the regression analysis of rate of population growth and slope at the origin ($\tilde{\alpha}$) at minimum population size versus bottom temperature with the robust estimate of the slope, and found simi-

Table 2

For each of the three variables r_m(population growth rate), $\tilde{\alpha}$ (standardized slope of the spawner-recruit curve at the origin), and a (age-at-maturity), the estimated slope parameter of the regression on temperature (T) (e.g. $r_m = a + bT$) is presented, labeled $\hat{b}$. For r_m and $\tilde{\alpha}$, there are two b values based respectively on the Ricker fit to each spawner-recruit data set and the median of the first six points of each spawner-recruit data set. Also shown are the significance levels of the regressions on temperature and the corresponding r^2. The results are presented for the Northwest, Northeast, and entire Atlantic.

Variable	Ricker $\hat{b}$	Ricker $P(b=0)$	Ricker r^2	Median $\hat{b}$	Median $P(b>0)$	Median r^2
r_m						
West	0.04	0.001	0.63	0.02	0.03	0.51
East	0.09	0.003	0.64	0.04	0.06	0.35
All	0.06	0.00008	0.59	0.04	0.00003	0.62
$\tilde{\alpha}$						
West	0.32	0.5	0.06	−0.16	0.3	0.15
East	0.83	0.2	0.16	0.09	0.7	0.02
All	0.67	0.04	0.21	0.13	0.2	0.08
a						
West	−0.62	0.00005	0.92	—	—	—
East	−0.45	0.06	0.34	—	—	—
All	−0.47	0.00002	0.65	—	—	—

lar results to those using the Ricker model (Table 2; Fig. 9). We conclude that our results are robust in relation to the method used to estimate $\tilde{\alpha}$.

Discussion

Perhaps remarkably, our study has revealed that the allometric (cross species) approximate inverse proportionality between r_m and age-at-maturity holds within the species Atlantic cod. Despite the much narrower range of r_m used in our single-species comparison (in contrast to the wide variation in r_m found in cross-species studies), the relation between r_m and age-at-maturity prevails over other influences. The expectation that cod populations at the northern and southern extremes of their range should show higher resilience (r_m), because of greater susceptibility to environmental change (Myers, 1991), is not realized.

In a similar vein, Roff (1984) suggested that early maturity in fish species may arise through *r*-selection (in response to extreme environmental variability); our findings show that age-at-maturity appears to be chiefly explained by ambient temperature.

Although we have found a clear relation between r_m and temperature, this was not necessarily expected a priori because mortality is positively related to temperature in comparative studies (Pauly, 1980). That temperature dependent (egg to adult) mortality can offset the effect of temperature-dependent growth is emphasized by the temperature independence of $\tilde{\alpha}$. More specifically, $\tilde{\alpha}$ depends on both fecundity and mortality. Fecundity, being growth dependent (Roff, 1984) increases with temperature; however, mortality also increases with temperature and counteracts the influence of temperature-dependent growth, leaving $\tilde{\alpha}$ temperature independent. (Note that many empirical studies of life histories of fish have found that somatic growth rate and survival covary [Beverton and Holt, 1959; Pauly, 1980; Myers and Doyle, 1983; Hutchings, 1993]).

The relation between r_m and temperature is presumably a metabolic effect, in that fish growth is strongly influenced by temperature (Taylor, 1958; Pauly, 1980), and implies that a fish in a warm environment will reach the required size for maturity at an early age, which tends to increase r_m. Although Birch (1948) has noted, for insect populations, that higher r_m values do not necessarily correspond to higher temperatures, investigators such as Hennemann (1983) and McNab (1980) have suggested that r_m should be closely related to metabolic rate, which is closely linked to temperature. Certainly our presentation corroborates this proposed parallel between metabolism and r_m.

The importance of the determination of r_m has long been known (Lewontin, 1965); however, it is certainly not always the case that age-at-maturity is the dominant factor. For species for which the production of replacement adults at low population density, $\tilde{\alpha}$, is relatively low (e.g. for many mammals and birds), then changes in $\tilde{\alpha}$ or adult survival will have large effects on r_m (Fig. 1). However, for cod, and perhaps many fish, $\tilde{\alpha}$ is relatively large (e.g. around 4). In this case, the effects of reasonable changes in adult

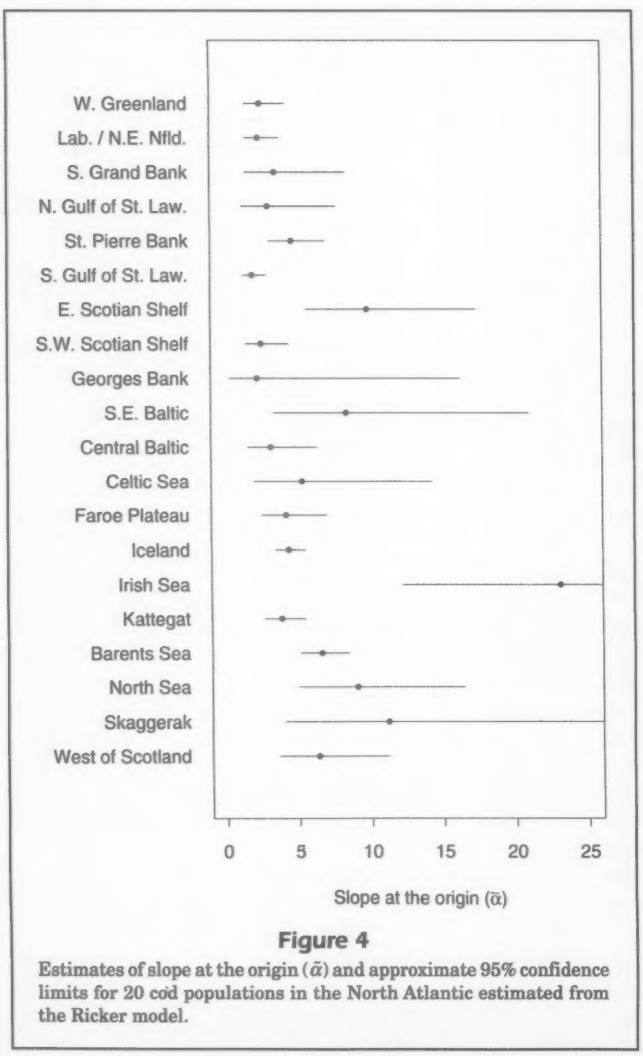

Figure 4

Estimates of slope at the origin ($\tilde{\alpha}$) and approximate 95% confidence limits for 20 cod populations in the North Atlantic estimated from the Ricker model.

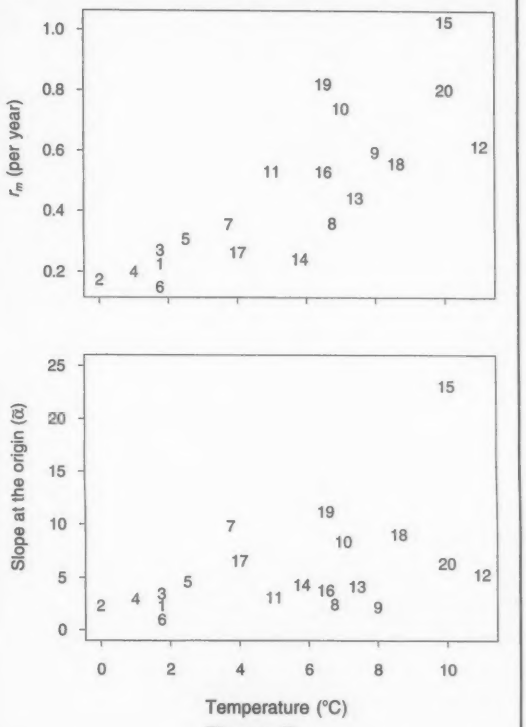

Figure 5

Rate of population growth (r_m) and slope at the origin ($\tilde{\alpha}$) versus bottom temperature. Populations are represented by numbers (See Table 1).

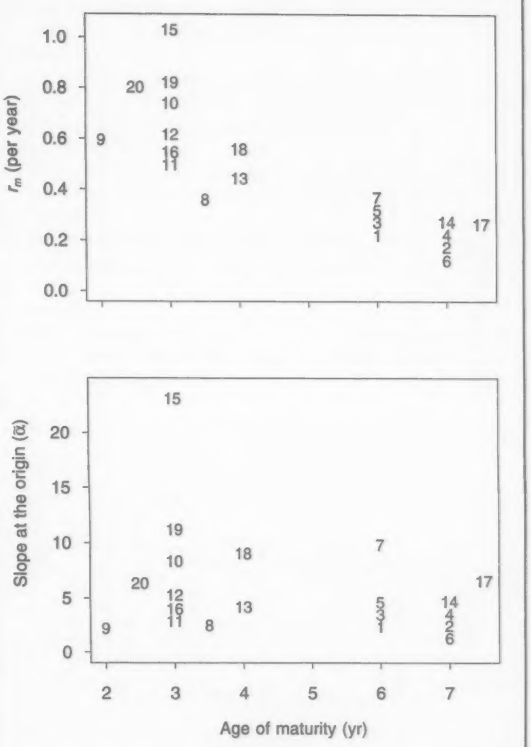

Figure 6

Rate of population growth (r_m) and slope at the origin ($\tilde{\alpha}$) versus age of maturity (a). Populations are represented by numbers (See Table 1).

survival (between 0.7 to 0.9) or $\tilde{\alpha}$ have a relatively small effect compared with age-at-maturity (Fig. 1).

Our study has presented robust estimates (see Fig. 8) of r_m for a variety of Atlantic cod populations, thus establishing recovery times for overfished populations relieved from fishing pressure. At colder temperatures, r_m is around 18% a year for all populations, independent of how we calculate r_m.

A major source of uncertainty in the SPA estimates of recruitment and SSB used in our analysis is that catches are assumed to be known without error. This assumption is particularly important when estimates of discarding and misreporting are not included in the catch-at-age data used in the SPA.These errors are clearly important for some periods of time for some of the cod stocks (Myers et al., 1997), and these errors will affect our estimates of the number of replacements each spawner can produce at low population densities ($\tilde{\alpha}$). However, we have shown that the estimates of r_m are not very sensitive to reasonable changes in this parameter.

We have carried our estimation of the model parameters separately for each stock. An alternative approach is to analyze simultaneously all stocks in models that include separate estimation error for each stock and a parameter describing the variation among stocks. Myers et al.[1] carried out such an analysis using variance components models for the data analyzed in this study and found that the optimal estimates of the variation in $\tilde{\alpha}$ was much less than that estimated, e.g. the very high estimate for Irish Sea cod was found to be overestimated.

The parameters estimated in this study have management implications that go beyond the estimation of population growth rate. In particular, the number of replacements each spawner can produce at low population densities ($\tilde{\alpha}$), is critical for determining

[1] Myers, R., G. Mertz, and N. Barrowman. 1996. Invariants of spawner-recruitment relationships for marine, anadromous, and freshwater species. ICES Council Meeting 1996 /D:11, 17 p.

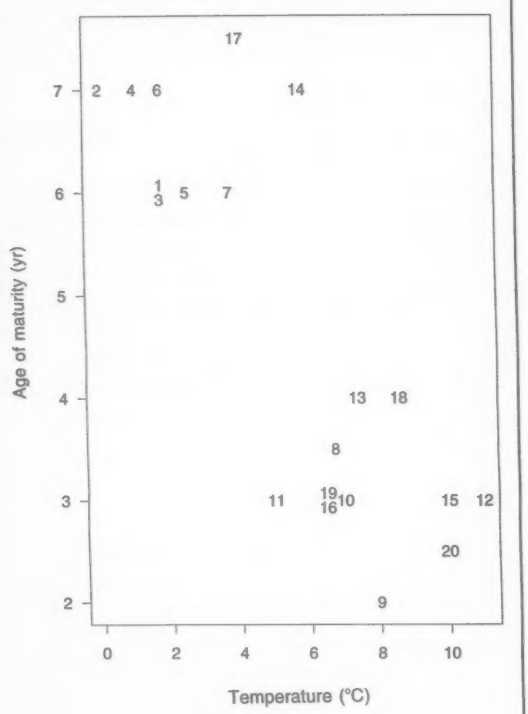

Figure 7

Age at maturity (a) versus bottom temperature. Populations are represented by numbers (See Table 1).

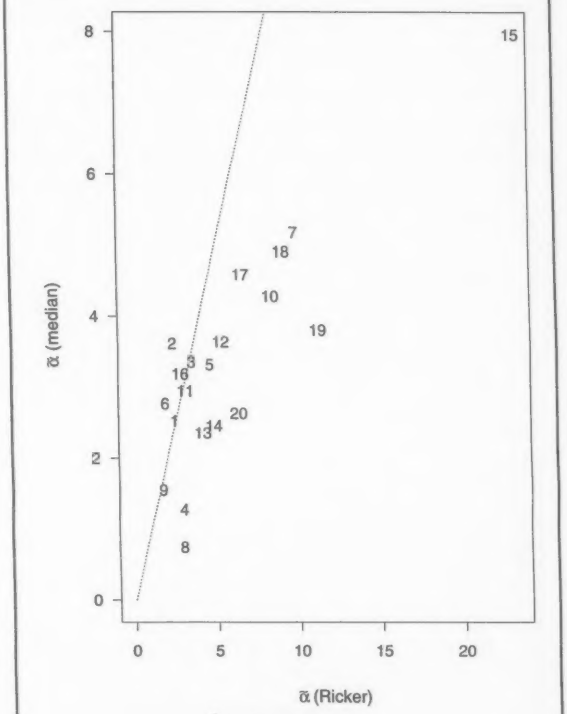

Figure 8

Comparison of slope at the origin ($\tilde{\alpha}$) calculated as the median slope of the six observations with the lowest SSB with that estimated from the Ricker model. Populations are represented by numbers (See Table 1).

the limits of exploitation (Cook et al., 1997; Myers and Mertz, in press). A comparative approach, such as the one used here, should help refine our understanding of the rational exploitation of fisheries.

We have used as simple a model as possible to estimate r_m. This has the very great advantage that the we can compare the crucial demographic parameters (i.e. the replacements each spawner can produce at low population densities ($\tilde{\alpha}$), age-at-maturity (a), and adult survival (p_s) among populations) and can easily study the sensitivity of r_m to errors in each of these parameters (Fig. 1). Furthermore, Hutchings and Myers (1994) found similar estimates of r_m when they used a fully age-structured model for "northern" cod, i.e. cod in NAFO Division 2J3KL.

Previous estimates of the recovery time for depleted cod stocks that have not included a detailed analysis of population growth rate have yielded widely different results. For example, it was initially projected that northern cod would recover close to historic levels of spawning biomass after a two-year fishing moratorium (Lear and Parsons, 1993). This projection has since been shown to be incorrect (Myers et al., 1996; Hutchings et al., 1997). Roughgarden and Smith (1996) estimated r_m for northern cod to be ≈1 by simply taking the greatest difference between adjacent estimates of total population abundance from annual research vessel surveys. That is, they assumed that any change in the estimates represented an increase in population abundance.

However, this change in estimated abundance was almost entirely estimation error (Myers and Cadigan 1995, a and b) and had nothing to do with an increase in abundance. At present (March 1997) there are six Canadian cod populations (2 to 7 in Table 1) that are currently protected by a fishing moratorium because the populations have been greatly reduced by overfishing (Myers et al., 1997). Unfortunately, our results indicate that recovery could require a long period. Under average environmental conditions, our results suggest a doubling time of about 4 years. Given the severe depletion of these populations (some are less than 5% of their maximum observed levels (Myers et al., 1996) recovery to

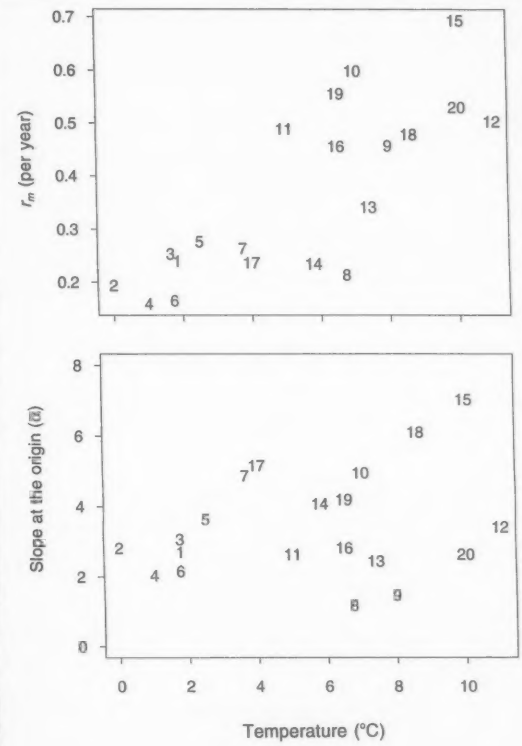

Figure 9

Rate of population growth (r_m) and slope at the origin (α) versus bottom temperature with estimated from the median slope of the six observations with the lowest SSB. Populations are represented by numbers (See Table 1).

desired levels of spawning biomass should not be expected for at least a decade of minimal mortality caused be fishing.

Acknowledgments

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Age and growth of larval and juvenile Atlantic croaker, *Micropogonias undulatus*, from the Middle Atlantic Bight and estuarine waters of Virginia

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Abstract.—Sagittal otoliths were used to determine age and growth of 605 larval and juvenile Atlantic croaker, *Micropogonias undulatus*, collected in the Middle Atlantic Bight and estuarine waters of Virginia. This study is the first to use age-based analysis for young Atlantic croaker collected in this region. A Laird-Gompertz model (r^2=0.95) was used to describe the growth of Atlantic croaker up to 65 mm standard length (SL) and 142 days (t): $SL_{(t)} = 2.657 \exp\{4.656[1-\exp(-0.0081t)]\}$; where $SL_{(t)}$ = standard length at day t. Spatial and temporal patterns in the size and age of Atlantic croaker showed a pattern of inshore immigration from offshore spawning grounds, and faster early-season growth compared with late-season growth. Back-calculated hatching dates of Atlantic croaker collected in Virginia estuaries indicated a protracted spawning period over 8 months, from early July 1987 to early February 1988, with at least 82% of spawning occurring from August to October. Regression analysis indicated that early-spawned larvae (July through August) grew more than 39% faster than late-spawned larvae (September through February). Lapillar and sagittal otoliths were compared with light microscopy; ages were underestimated with lapillar otoliths, which were particularly inadequate in determining the age of older juveniles. The relation between SL and sagittal otolith maximum diameter was best described by a fourth order polynomial (r^2=0.99) and faster-growing Atlantic croaker had larger otoliths (12%) than the same size slower-growing fish.

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Fishery Bulletin 95:773–784 (1997).

Atlantic croaker, *Micropogonias undulatus*, range from New York to Florida and along the western and northern Gulf of Mexico (Ross, 1988; Atlantic States Marine Fisheries Commission, 1993). Historically, Atlantic croaker have ranked as one of the top five species in the commercial catch of finfishes in the middle Atlantic region (McHugh and Conover, 1986), although recruitment is highly variable in the species. In Virginia, annual commercial landings have varied by as much as threefold and have apparently declined overall since 1937 (Chesapeake Bay Program, 1988). Similarly, recreational landings have varied by as much as twofold over two years (U.S. Department of Commerce, 1991).

In species with substantial annual recruitment variability, change in the survival rate of prerecruits (larvae and juveniles) is a key factor in determining adult abundance (Houde, 1987). Determination of survival rates of prerecruits relies, in part, on daily age and growth information (Jones, 1992), and although otolith daily increment analysis has become common practice (Jones, 1992), there are few published age and growth studies on the early life history of Atlantic croaker. Furthermore, there are no age-based estimates of growth for larval and juvenile Atlantic croaker for the Middle Atlantic Bight (MAB: shelf waters from Long Island, NY, to Cape Hatteras, NC) and estuarine waters of Virginia. Comparable age-based studies on the early life history of Atlantic croaker have concentrated on larvae collected in coastal waters south of Cape Hatteras, North Carolina (Warlen, 1982), or the northern Gulf of Mexico (Cowan, 1988).

North Carolina larvae (Warlen, 1982), collected south of Cape Hatteras at Beaufort Inlet, show a twofold decline in length-at-age between early- and late-season collections. Likewise, Cowan (1988) shows a similar slow growth rate for late-season larvae collected in the northern Gulf of Mexico. Warlen's (1982) back-calculated hatching dates indicate a broad spawning season from September to February, with peak spawning in October and November. On the basis of the pattern of progressive increase in mean size and age from the shelf to the estuary and on the basis of seasonal

variability in age of larvae entering the estuary, Warlen (1982) postulates two offshore spawning locations for Atlantic croaker entering Beaufort. Warlen's conclusions imply potential differences in spawning source between larvae entering Chesapeake Bay and some of those entering Beaufort Inlet.

The purpose of the present study was to examine age and growth of larval and juvenile Atlantic croaker from the MAB and estuarine waters of Chesapeake Bay by using daily growth rings on otoliths. Specifically, we investigated the variability of size, size and age of entry into Chesapeake Bay, calculated hatching-date distributions to estimate spawning periodicity, and estimated temporal and spatial differences in growth rates. In addition, we determined if there were significant differences in age counts between lapillar and sagittal otoliths and in size and age counts between left and right sagittal otoliths. Finally, we compared the relation between otolith growth and somatic growth for field-captured Atlantic croaker with results presented in the literature.

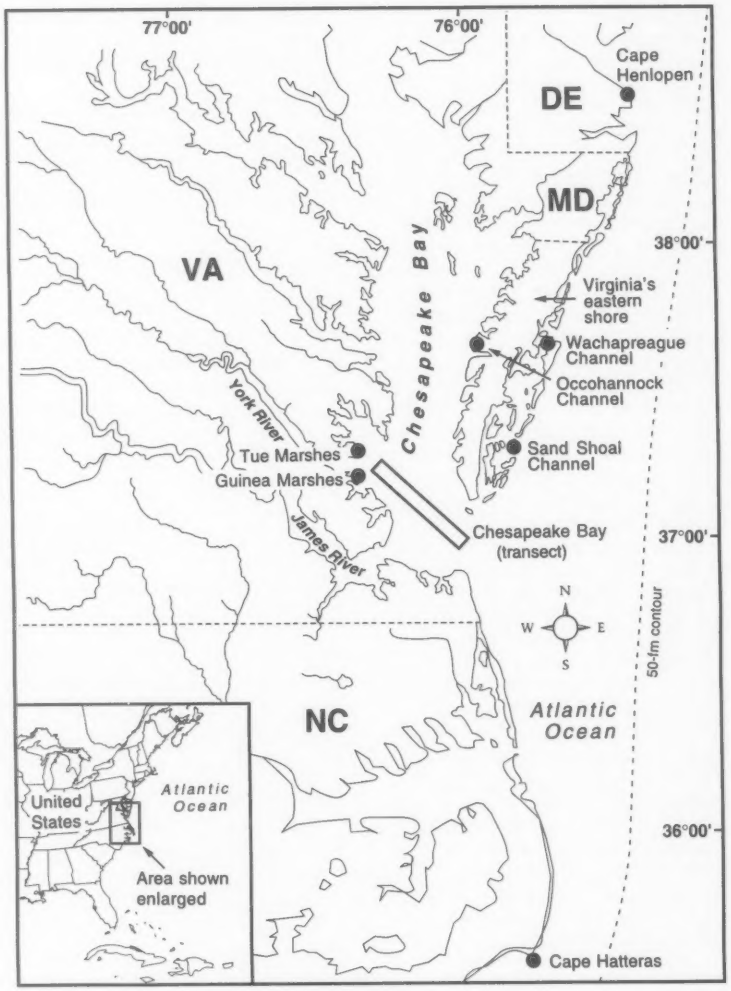

Figure 1

Station locations in estuarine waters of Virginia for collection of larval and juvenile Atlantic croaker from 21 September 1987 to 30 March 1988.

Materials and methods

Sampling regime

Larval Atlantic croaker were collected in the MAB (from Cape Henlopen, Delaware, to Cape Hatteras, North Carolina; Fig. 1) from 3 November to 14 November 1987 from the shore to the 91-m (50-fm) contour with a stratified grid system illustrated in the MARMAP Plankton Survey Manual (Jossi and Marak, 1983). Seven additional stations at 2-km intervals were sampled along a transect across the mouth of the Chesapeake Bay. Larvae were sampled in oblique tows with a 60-cm bongo sampler containing 505-µm mesh. Larval and juvenile Atlantic croaker sampled by Norcross and Hata (1990) were collected monthly from 29 September 1987 to 10 March 1988 at three inshore stations at Virginia's Eastern Shore (Wachapreague, Sand Shoal, and Occohannock Channel) and at two stations at the mouth of the York River (Guinea and Tue Marshes; Fig. 1) with two 4.9-m otter trawls (one lined, one unlined) towed simultaneously. The lined net had a 6.4-mm mesh and a 3.2-mm mesh liner, and the unlined net a 15.9-mm mesh. Additional larval and juvenile Atlantic croaker were collected monthly from 21 September 1987 to 1 February 1988 at 8.1-km intervals along a 40.2-km transect running from the mouth of the York River to the mouth of the Chesapeake Bay (Fig. 1) with an otter trawl with a 9.1-m lined net containing 15.9-mm mesh and a 6.4-mm mesh liner. Finally, juvenile Atlantic croaker sampled by Dameron et al.[1] were collected monthly from 25 January to 30 March 1988 in the channels of the York and James Rivers at 8.1-km intervals from the mouth of the two rivers to 56.3 km upstream (Fig. 1) with

an otter trawl with a 9.1-m lined net containing 15.9-mm mesh and a 6.4-mm mesh liner. Otter trawls were towed at 1.0 to 1.5 m/s over the bottom for five minutes. Specimens were preserved in 70% ethanol immediately upon collection. The ethanol was changed within 24 hours and again after two days.

Otolith processing and data analysis

Standard length (SL) measurements were made on fish to the nearest 0.1 mm with an image analysis system for individuals <20 mm SL or with vernier calipers for individuals ≥20 mm SL. Sagittal and lapillar otoliths were extracted from at least 30 fish chosen at random from each station and sampling date (n=605, 40 from the MAB and 565 from estuarine waters). Otoliths were extracted from all individuals when samples contained less than 30 fish. Only 40 of the 126 larvae collected in the MAB were available for age analysis owing to inadequate preservation. Otolith maximum diameter (OMD) was measured on sagittae from rostrum to postrostrum to the nearest 0.1 mm with an image analysis system—39 otoliths from larvae collected in the MAB and 143 otoliths from randomly selected estuarine larvae and juveniles were measured.

The right sagittal otolith was used in age and growth analyses except when lost or damaged; then the left otolith was used. Procedures for the preparation of otoliths that required sectioning and polishing followed Epperly et al. (1991)—in short, otoliths were sectioned longitudinally, ground, and then polished to the primordia on both sides. Generally, otoliths from fish <15 mm SL did not require grinding or polishing to distinguish daily increments; they were placed directly on glass slides and embedded in Euparal. Otoliths were read at 1,000×, under cross-polarized, transmitted light on a monitor with an image analysis system. All specimens were aged without knowledge of fish size or collection date. Three independent age counts were averaged to determine final ages. Age counts were estimated by adding 5 days to the number of daily increments in the otoliths by assuming that increment deposition begins at 5 days posthatching as in spot (*Leiostomus xanthurus*; Peters et al.[2]).

[1] Dameron, J. C., P. J. Geer, C. F. Bonzek, and H. M. Austin. 1994. Juvenile finfish and blue crab stock assessment program, bottom trawl survey. Annual data summary report series vol. 1987. Special Scientific Report 124, Virginia Institute of Marine Science, College of William and Mary, Gloucester Pt., VA.

[2] Peters, D. S., J. C. Devane Jr., M. T. Boyd, L. C. Clements, and A. B. Powell. 1978. Preliminary observations of feeding, growth, and energy budget of larval spot (*Leiostomus xanthurus*). *In* Annu. Rep. NMFS, Beaufort, NC, p. 377–397.

Paired t-tests were used to determine if there were significant differences in age estimates between lapillar and sagittal otoliths (n=32) and in size and age counts between left and right otoliths (n=30). Also, the precision of sagittal age counts by the primary reader and a secondary reader were compared (n=50) with the indices of average percent error (Beamish and Fournier, 1981), coefficients of variation, and index of precision (Chang, 1982). A paired t-test also was used to determine if there was a significant difference in mean age counts between readers.

To generalize comparisons of mean growth rates and size-at-age of Atlantic croaker across capture sites, stations were grouped geographically into regions. These regions were designated as MAB, Chesapeake Bay, seaside Eastern Shore (includes the Wachapreague and Sand Shoal Channel stations), bayside Eastern Shore (includes the Occohannock Channel station), marshes (includes the Tue and Guinea marsh stations), and rivers (includes the James and York river transects). The length and age of fish were compared among regions sampled with similar gears with independent, two-sample t-tests.

Linear regression comparisons (Rawlings, 1988) were used to compare growth rates (slopes) and size at day 0 (y-intercepts) between early- (September through October) and late-captured (November through March) larvae ≤15 mm SL and ≤80 d. The analysis was restricted by size because larger, older juveniles were not available during early-season collections. Linear regression comparisons (Rawlings, 1988) were also used 1) to compare growth between early- (July through August) and late-season (September through February) spawned larvae (≤19 mm SL) and 2) to compare growth between early- and late-season spawned juveniles (19.1–65 mm SL). Early- and late-spawned larvae and juveniles were analyzed separately so that linear growth patterns could be described for the two life stages. We also used ANCOVA to compare mean size between early- and late-spawned juveniles.

A Laird-Gompertz growth model (Laird et al., 1965) was used to describe the growth of Atlantic croaker larvae and juveniles ≤50 mm SL and ≤142 d:

$$SL_{(t)} = SL_{(0)}/\exp\{[A_{(0)}/\alpha][1 - \exp(-\alpha t)]\};$$

$SL_{(t)}$ = standard length at day t;
$SL_{(0)}$ = assumed standard length at hatching (t=0);
$A_{(0)}$ = specific growth rate at hatching (t=0); and
α = rate of exponential decay of the specific growth rate.

The model was fitted by an iterative, nonlinear least-squares procedure. Age-specific growth rates were subsequently calculated as

$$A_{(t)} = A_{(0)} \exp(-\alpha t).$$

Finally, ANCOVA was used to compare mean otolith size between early-captured, fast-growing Atlantic croaker with late-captured, slower-growing Atlantic croaker between 11 and 37 mm SL.

Results

Otolith analysis

Age counts in sagittal and lapillar otoliths were significantly different (t-test, P=0.002). For older age fish, lapillar counts underestimated sagittal counts, and the disparity increased with increasing age (Fig. 2). Also, no differences were found among size (t-test, P=0.49) and age counts (t-test, P=0.85) between left and right sagittal otoliths (n=30).

Sagittal age counts by the primary reader showed good precision —the average percent error (APE) of counts was 4.8%, with a coefficients of variation (CV) and index of precision (D) of 6.4% and 3.8%, respectively. For the second reader's age counts these indices were 8.4% (APE), 11.5% (CV), and 6.7% (D). Although the second reader's age counts had relatively low precision, there was no significant difference in mean age counts between readers (t-test, P=0.27).

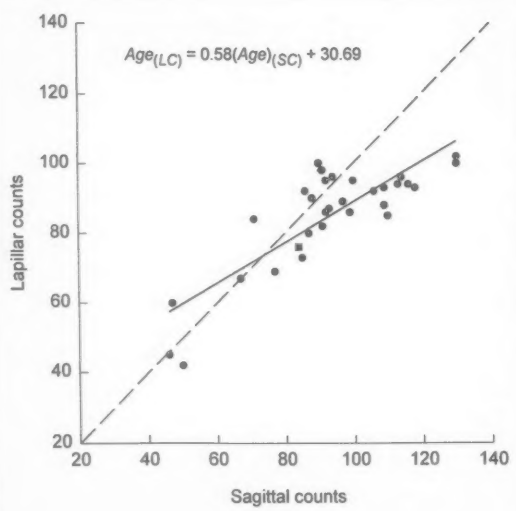

Figure 2

Comparison of sagittal and lapillar otolith age counts (r^2=0.73, n=32) illustrating reproducibility of sagittal counts (Age_{SC}) with lapillar counts (Age_{LC}). Dashed line represents a one-to-one relation, and the solid line the regression describing the relation between sagittal and lapillar age counts.

Size and age distributions

Monthly length- and age-frequency distributions showed that size and age of fish generally increased from September to January (Fig. 3). Size and age appeared to decline in February (although sample sizes were small) and mostly represented fish collected in the rivers after January. Also, length distributions were highly variable in comparison with respective age distributions (Fig. 3). For example, fish collected in November had two distinct length modes, whereas their age frequencies clearly had only one mode. This pattern was also evident for fish collected in October and January; thus size does not appear to be a good predictor of age in these fish.

Generally, smaller and younger fish were found in the seaside Eastern Shore region compared with the bayside Eastern Shore or marsh regions (t-tests, P<0.001) over the entire sampling season. This pattern was evident regardless of gear type. Significantly smaller (P=0.02) and younger (P<0.001) fish were found in the mainstem Chesapeake Bay compared with the rivers inland of the Bay. However, the rivers were sampled only during the later half of the sampling period.

The age of larval Atlantic croaker entering Virginia nursery grounds was examined from specimens collected at the mouth of the Chesapeake Bay (the most seaward station along the Chesapeake Bay transect) and at Wachapreague and Sand Shoal Channels. The youngest larvae (24 d) entered the mouth of the Chesapeake Bay on 21 September 1987 and measured 6.1 to 7.6 mm SL (n=3). Fish collected at Wachapreague and Sand Shoal Channels were probably better representatives of the age of larvae that enter Virginia nursery grounds because smaller mesh nets (with 3.2-mm mesh liner which sampled smaller larvae more effectively) were used at these stations. The youngest larvae observed at Wachapreague Channel were collected on 29 September 1987 with a mean size and age of 7.3 mm SL and 26 d, respectively, with the youngest individuals (20 d) measuring 5.4 and 6.1 mm SL (n=2). The youngest larvae observed at Sand Shoal Channel were collected on 30 September 1987 with a mean size and age of 8.3 mm SL and 29 d, respectively, with the youngest individuals (23 d) measuring 6.1 and 7.3 mm SL (n=2). In conclusion, it appeared that the youngest larvae entered Virginian estuaries at an approximate age of 20 to 26 d, measuring 5.4 to 7.6 mm SL.

Hatching-date distributions

Hatching-date distributions indicated a protracted spawning period of 8 months from 5 July 1987 to 10 February 1988 and with 82% of spawning limited to

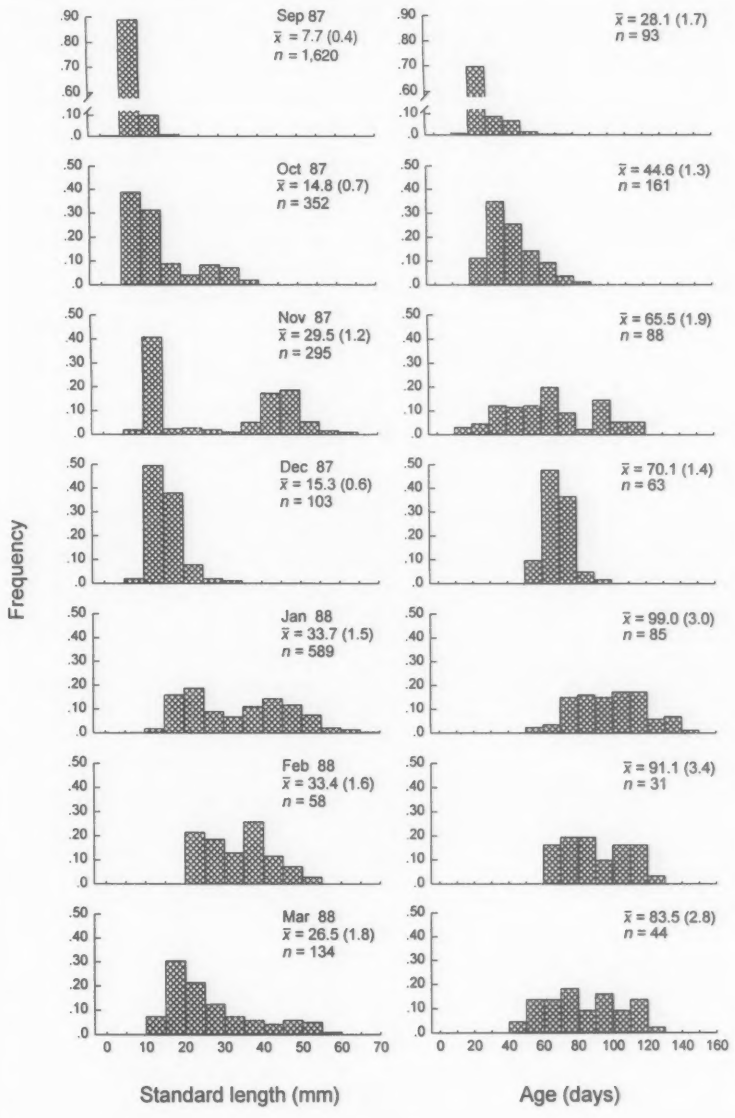

Figure 3

Monthly length- and age-frequency distributions for larval and juvenile Atlantic croaker collected from 21 September 1987 to 30 March 1988 in estuarine waters of Virginia. Also given are mean standard length and standard error in parentheses, ages and standard error in parentheses, and sample size (n).

August through October. Fish spawned earlier in the season are underrepresented in samples because they have experienced greater cumulative mortality than later spawned fish (Campana and Jones, 1992). Estimates of size- and age-specific mortality are needed to predict hatching-date distributions more accurately, and these were not available. However, the result of greater accumulated mortality on early-spawned fish is to minimize the height of the estimated spawning peak. Hence, our results establish a lower bound of 82% of surviving juveniles spawned from August to October.

Growth

Mean growth rates (mean SL divided by mean age) varied from 0.18 mm/d in the MAB to 0.41 mm/d in Chesapeake Bay (Table 1). Furthermore, early-spawned fish experienced considerably faster growth than late-spawned fish (Table 1).

Early-captured larvae grew 37% faster than late-captured larvae for individuals ≤15 mm SL and ≤80 d (Fig. 4A). Early-captured individuals were larger at age than late-captured individuals because of different growth rates and not because of larger size at hatching, as indicated by tests of regression coefficients that showed highly significant differences between slopes ($P<0.001$) but not between intercepts ($P=0.16$).

Early-spawned larvae grew 39% faster than late-spawned larvae (Fig. 4B), and once these size differences were established, they persisted through the juvenile stage (Fig. 4C). There was a significant difference between slopes ($P<0.001$) for early- and late-spawned larvae, whereas, early- and late-spawned juveniles experienced similar growth according to tests of regression coefficients ($P=0.75$). Furthermore,

Table 1

Mean standard length (mm) and standard error (SE), age (d) (SE), and growth rate (mean SL/mean age) for larval and juvenile Atlantic croaker collected in the Middle Atlantic Bight and estuarine waters of Virginia from 21 September 1987 to 10 March 1988 by hatching month, region, and gear type.

Hatching month	Sample size	Mean standard length ± SE	Mean age ± SE	Mean growth
Middle Atlantic Bight (MAB)[1]				
Sep	19	7.9 ± 0.2	43.7 ± 0.9	0.18
Oct	21	5.8 ± 0.4	29.7 ± 1.5	0.20
Seaside Eastern Shore (SES: Wachapregue and Sand Shoal Channel)[2]				
Aug	17	13.2 ± 1.5	41.0 ± 3.8	0.32
Sep	115	11.0 ± 0.5	42.7 ± 1.8	0.26
Oct	6	13.6 ± 0.8	56.5 ± 1.1	0.24
Bayside Eastern Shore (BES: Occohannock Channel)[2]				
Aug	1	28.3 ± 0.0	94.0 ± 0.0	0.30
Sep	32	14.4 ± 0.7	67.1 ± 1.2	0.21
Oct	15	11.0 ± 0.2	57.5 ± 0.7	0.19
Chesapeake Bay[3]				
Jul	7	25.8 ± 6.5	77.3 ± 11.2	0.33
Aug	74	28.9 ± 2.0	70.5 ± 3.8	0.41
Sep	21	27.8 ± 3.4	78.4 ± 8.0	0.36
Oct	21	35.4 ± 1.7	94.2 ± 2.7	0.38
Nov	7	20.4 ± 1.3	71.6 ± 1.0	0.29
Marshes (Guinea and Tue Marshes)[2]				
Jul	10	24.0 ± 2.4	71.2 ± 3.0	0.38
Aug	39	16.5 ± 1.2	48.6 ± 2.2	0.34
Sep	75	9.8 ± 0.3	47.0 ± 2.2	0.21
Oct	4	10.6 ± 0.6	60.0 ± 1.0	0.18
Jan	7	12.7 ± 0.4	54.7 ± 2.0	0.23
Rivers (York and James River)[3]				
Sep	13	48.5 ± 2.2	124.3 ± 1.7	0.39
Oct	25	32.1 ± 2.1	105.3 ± 2.2	0.30
Nov	28	27.6 ± 2.0	91.5 ± 2.8	0.30
Dec	32	31.8 ± 2.2	89.5 ± 2.9	0.36
Jan	15	24.4 ± 1.7	74.4 ± 1.4	0.33
Feb	1	10.6 ± 0.0	49.0 ± 0.0	0.22

[1] Gear type used was oblique 60-cm bongo nets with 505-μm mesh.
[2] Gear type used was a 4.9-m lined trawl net with a 6.4-mm mesh and 3.2-mm mesh liner and a 4.9-m unlined net with a 15.9-mm mesh. The lined and unlined nets were towed simultaneously.
[3] Gear type used was a 9.1-m lined trawl net with a 15.9-mm mesh and 6.4-mm mesh liner.

early-spawned juveniles were significantly larger (18%) than late-spawned juveniles when mean size was adjusted by age (ANCOVA, $P<0.001$, Table 2B).

A Laird-Gompertz growth model fitted the entire range of Virginia data well ($r^2=0.95$), although variance in size increased with age (Fig. 5). Standard length at hatching ($SL_{(0)}$) estimated from the Laird-Gompertz growth model (Fig. 5) was 2.7 ±0.3 mm SL and was similar to size-at-hatching estimates for laboratory-spawned Atlantic croaker from the Chesapeake Bay (2.0 mm SL; Middaugh and Yoakum, 1974) and North Carolina (2.4 mm SL; Jones[3]), but considerably higher than Warlen's (1982) estimate of 0.9 mm SL for wild-captured Atlantic croaker larvae from North Carolina. The rate of exponential decay of the specific growth rate (α) was estimated at 0.0081 ± 0.0012 (Fig. 6). Changes in age-specific growth (A_t, a function of the rate of exponential decay of specific growth in time) indicated that larvae experienced a decline of daily growth rate from 3.2% at day 20 to 2.3% by day 60 (Fig. 6).

Standard length and otolith maximum diameter (OMD) relation

The relation between sagittal OMD and SL was best described by a fourth order polynomial (Fig. 7). A simple linear model also described the OMD and SL relation fairly well (SL = 13.5 (OMD) + 4.2, $r^2=0.98$); however, there were strong patterns in the residuals. Otolith growth was similar between early-captured (fast growers captured from September to October) and late-captured (slow growers captured from November to March) groups when compared by slope ($P=0.50$). However, a significant difference was observed between the two groups when otolith size was adjusted for fish size (ANCOVA, $P<0.001$, Table 3A). Size-adjusted means indicated that otoliths from the early-captured group were almost 13% larger than otoliths from the late-captured group (Table 3B). Plots of individual otoliths showed very little overlap between groups (Fig. 8).

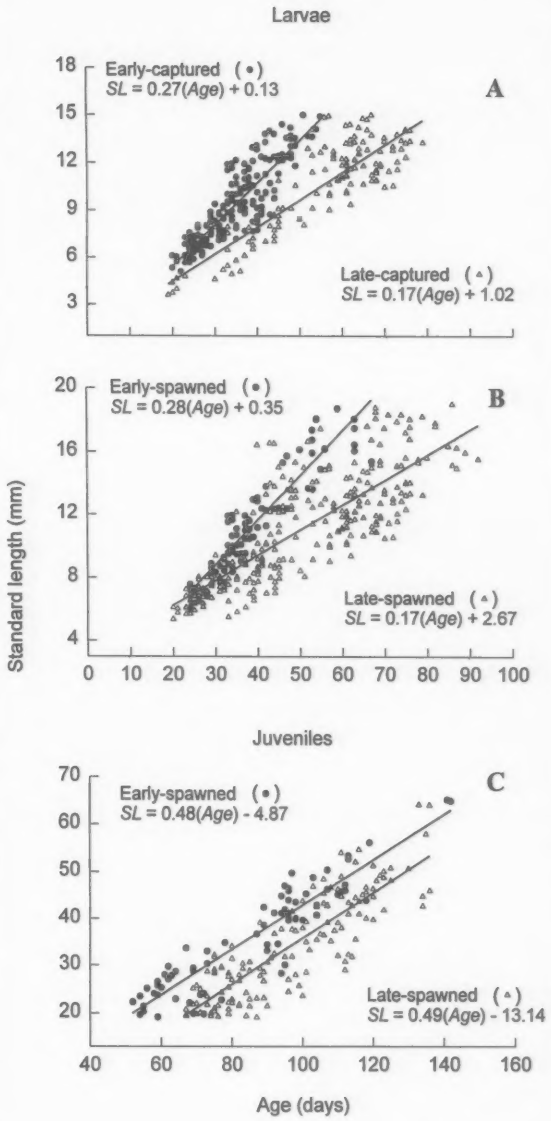

Figure 4

(**A**) Growth comparison between early- (September through October, $r^2=0.78$, $n=199$) and late-captured (November through March, $r^2=0.77$, $n=132$) Atlantic croaker ≤15 mm standard length (SL) and ≤80 d. (**B**) Growth comparison between early- (July through August, $r^2=0.92$, $n=77$) and late-spawned (September through February, $r^2=0.84$, $n=314$) Atlantic croaker up to 19 mm SL. (**C**) Growth comparison between early- ($r^2=0.92$, $n=71$) and late-spawned ($r^2=0.86$, $n=143$) Atlantic croaker from 19.1 to 65 mm SL and from 51 to 142 d.

Discussion

Otolith analysis

We were unable to obtain known-age Atlantic croaker to validate the assumption that incre-

[3] Jones, C. J. 1995. Applied Marine Research Laboratory, Old Dominion University, Norfolk, VA 23529. Unpubl. data.

ments form daily in larvae. However, daily growth increments have been validated in the otoliths of larval spot, *Leiostomus xanthurus*, a sciaenid relative of Atlantic croaker (Peters et al.[2]), and we assumed, therefore, that increment deposition is daily in Atlantic croaker. Peters et al.[2] also demonstrated that the first daily increment forms in the sagittae of spot at the time of first feeding, which occurs in spot about 5 d after hatching at 18 and 20°C (Powell and Chester, 1985); thus, we added 5 days to our increment counts.

Sagittal otoliths of Atlantic croaker begin to increase growth along their anterior and posterior axes during the late-larval stage, whereas lapilli maintain concentric growth through the juvenile stage, potentially making lapilli preferable when using otoliths to backcalculate growth. In examining the potential for using lapillar counts as a surrogate to sagittal counts, we found under light microscopy that lapillar counts increasingly underestimated sagittal counts as fish increased in age. The microstructure in sagittal otoliths also had better defined increments, leading us to assume that sagittal counts were more accurate predictors of age than lapillar counts. No differences in the size and age counts between left and right sagittal otoliths warranted the replacement of lost or damaged right otoliths with left otoliths.

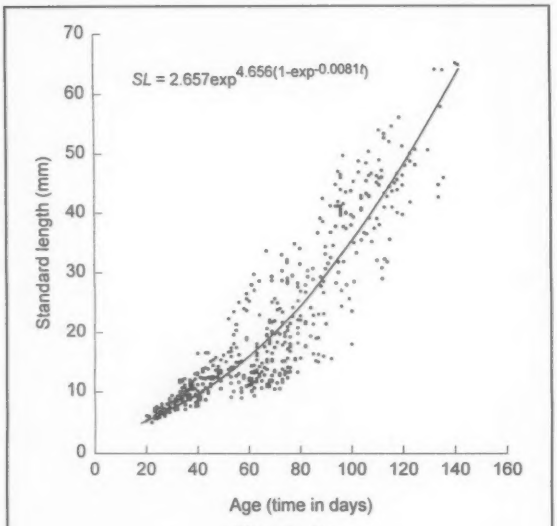

Figure 5

Laird-Gompertz growth model describing growth of Virginia larval and juvenile Atlantic croaker ≤65 mm standard length (SL) and ≤142 d (r^2=0.95, n=605).

Size and distribution

Offshore spawning and subsequent estuarine migration of Atlantic croaker have been thoroughly documented by studies with egg and larval size distributions (Hildebrand and Cable, 1930; Wallace, 1940; Haven, 1957; Colton et al., 1979; Morse, 1980; Lewis

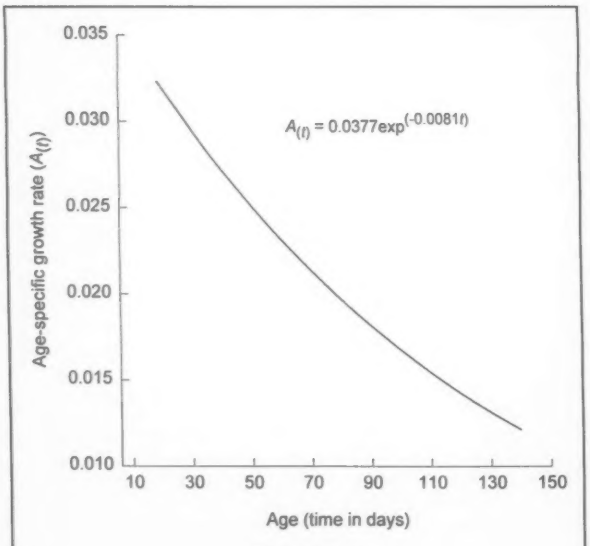

Figure 6

Age-specific growth rate relation determined from the equation $A_{(t)} = A_{(0)} \exp(-\alpha t)$ with $A_{(0)}$ and alpha from the Laird-Gompertz growth equation (Fig. 2).

Table 2

Growth comparison between early- (July through August) and late-spawned (September through February) Atlantic croaker from 19.1 to 65 mm SL and from 51 to 142 d with an analysis of covariance (ANCOVA) of standard length (SL) of fish (mm), with age (d) as the covariate. Size adjusted means equals the mean SL of fish, adjusted for the effects of age.

	ANCOVA		
A	df	*F*-value	*P*-value
Covariate age	1	743.6	$P<0.001$
Main effect Early-spawned vs. late-spawned	1	89.9	$P<0.001$
Residual sums of squares (d)	5,489.2 (211)		
r^2	0.78		

B	Size adjusted means (mm) (SE)
	Early-spawned: 39.5 (0.6) Late-spawned: 32.3 (0.4)

Table 3

Otolith comparison between faster-growing early-captured (September through October) Atlantic croaker and slower-growing late-captured (November though March) Atlantic croaker between 11 and 37 mm standard length (SL) with an analysis of covariance (ANCOVA) of the otolith maximum diameter (OMD) of sagittae (mm), with SL of fish (mm) as the covariate. Size-adjusted means equals the mean OMD of sagittae, adjusted for the effects of SL of fish.

	ANCOVA		
A	df	*F*-value	*P*-value
Covariate standard length	1	1,126.9	$P<0.001$
Main effect			
Early-captured vs. late-captured	1	36.2	$P<0.001$
Residual sums of squares (d)	1.16 (66)		
r^2	0.95		

B	Size adjusted means (mm) (SE)
	Early-captured: 1.54 (0.02) Late-captured: 1.25 (0.02)

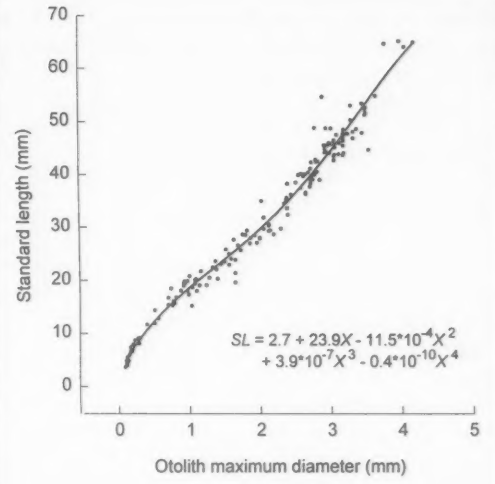

Figure 7

The relation between otolith maximum diameter (OMD) (mm) and standard length (SL) of fish (mm) (r^2=0.99, n=182).

and Judy, 1983; Warlen and Burke, 1990). However, only two studies (Warlen, 1982; this study) used daily age information from otoliths to support such findings. Daily age information is critical because size-at-age is highly variable in this species, and age-based data provide reliable confirmation of cross-shelf transport of larvae. Warlen (1982) found a general increase in the age of fish entering the Beaufort estuary as the season progressed, and suggested this increase in age was an effect of variable transport distance or rates to the estuary (or both). Seasonal trends observed in this study may be attributed to similar processes.

Mean ages generally increased over time, lagging about 10 d between monthly sampling dates, suggesting constant recruitment over the entire sampling season. However, mean ages in the rivers declined after December. Our samples collected in January along river transects show a gradient of smaller, younger individuals upstream and of larger, older individuals downstream. Bottom waters in the York River experience a winter temperature gradient, with the lowest temperatures occurring in upper reaches of the river (Chao and Musick, 1977; Dameron et al.[1]; Land et al.[4]) and the higher temperatures in the Bay mainstem. This bottom water temperature gradient coupled with the increase in size of Atlantic croaker

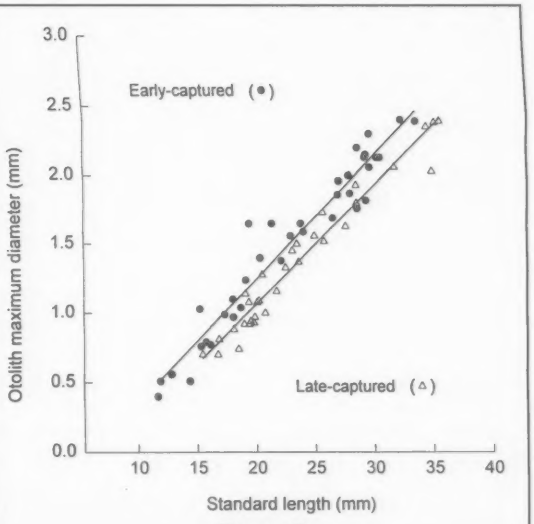

Figure 8

The relation between otolith maximum diameter (OMD) (mm) and standard length (SL) of fish (mm) illustrating otolith and somatic growth relation between faster-growing, early-captured (September through October) Atlantic croaker (n=36) and slower-growing, late-captured (November through March) Atlantic croaker (n=32) between 11 and 37 mm SL.

[4] Land, M. F., P. J. Geer, C. F. Bonzek, and H. M. Austin. 1994. Juvenile finfish and blue crab stock assessment program. Bottom trawl survey. Annual data summary report series. Volume 1988. Spec. Sci. Rep. Va. Inst. Mar. Sci., College of William and Mary, Gloucester Point, VA, 171 p.

downstream may indicate movement of larger, older individuals into deeper, warmer waters of the mainstem Chesapeake Bay. Atlantic croaker's sensitivity to low temperatures (Massmann and Pacheco, 1960; Joseph, 1972) may further explain the movement of older and larger fish from the rivers into warmer Bay waters.

Hatching-date distributions

Our estimate of a protracted spawning season from early July 1987 to February 1998, with peak spawning in September, is similar to earlier reports in studies that used the presence of eggs or early larvae to estimate spawning. These studies suggest a protracted spawning period from August through December with peak spawning from August to October (Wallace, 1940; White and Chittenden, 1977; Johnson, 1978; Colton et al., 1979; Morse, 1980; Chittenden et al.[5]). Although our observation that spawning may begin as early as July has not been reported elsewhere, ovaries containing postovulatory follicles recently have been observed in Atlantic croaker from the Chesapeake Bay as early as July (Barbieri et al., 1994). Furthermore, because sexually mature adults do not begin to migrate out of the Chesapeake Bay until early July, and mainly in August and September (Wallace, 1940), limited spawning of Atlantic croaker may occur in proximal coastal waters as suggested by Haven (1957).

Growth

When comparing temporal patterns in growth, it is best to analyze differences between groups by spawning date, rather than by capture date; otherwise older fish are under represented because of their greater accumulated mortality (Campana and Jones, 1992). Temporal growth variability was observed when the data were analyzed both by capture date and spawning date, although a 6% greater difference was observed when the data were analyzed by spawning date.

Seasonal variability in the growth of larval and juvenile Atlantic croaker may result from higher water temperatures or increased food in July and August (or both) (Alden et al.[6]) or from improved survival of larger, faster-growing fish (Miller et al., 1988; Isley and Grimes, 1996). Hatching dates of faster-growing, early-spawned fish coincided with peak mean surface water temperatures in July and August (26.3° and 26.7°C, respectively; U.S. Department of Commerce[7]) and with peak plankton abundances in the Chesapeake Bay which typically occur in July (Alden et al.[6]). Furthermore, hatching dates of slower-growing fish coincided with increased patchiness and falling plankton abundances which typically begin in September and October (Alden et al.[6]). Warlen (1982) reported similar seasonal growth patterns for North Carolina Atlantic croaker larvae and speculated that slow growth observed in late-captured fish (mid-January to mid-April) might be attributed to colder ocean temperatures and low food availability in mid- to late-winter, or less likely, to smaller egg size of late-spawned larvae.

Recently immigrated larvae collected in Virginia estuaries in this study were larger at age than North Carolina larvae. Monthly mean growth rates (mean SL/mean age) of estuarine collected larvae (26–65 d) in this study ranged from 0.26 to 0.40 mm/d and were considerably higher than weekly mean growth rates (0.16–0.27) for similar age (32–64 d) North Carolina larvae collected in estuarine waters (see Warlen 1982, Table 1). Because this study and Warlen's (1982) were conducted in different years, we cannot eliminate the real possibility that these differences may be temporal, year-to-year changes. Further inter-year studies within Virginia and North Carolina, showing consistent patterns of growth variability, are needed to conclude that there are regional growth differences. However, whether spatial or temporal, or a combination of both, within-season patterns among the two studies are similar, whereas growth rates themselves differ.

Apparently, Atlantic croaker larvae immigrating into estuaries of Virginia and North Carolina can be categorized as early-spawned, fast growers or as late-spawned, slow growers. These seasonal growth differences, coupled with a spatially and temporally extended spawning season suggest that Atlantic croaker encounter variable environmental factors that may affect their survival. Identifying factors that may enhance survival or affect mortality rates of these spatially and temporal explicit groups are of major interest and are worthy of further study.

[5] Chittenden, M. E., C. M. Jones, L. R. Barbieri, S. J. Bobko, and D. E. Kline. 1990. Initial information on the Atlantic croaker, a final report on development of age determination methods, life history-population dynamics information, and evaluation of growth overfishing potential for important recreational fishes. Final Rep. to Virginia Mar. Res. Comm. VMRC I, Va. Inst. Mar. Sci., College of William and Mary, Gloucester Point, VA, 88 p.

[6] Alden, R. W., III, R. S. Birdsong, D. M. Dauer, H. G. Marshall, and R. M. Ewing. 1992. Virginia Chesapeake Bay water quality and living resources monitoring programs: executive report, 1985–89. Applied Marine Research Laboratory, Old Dominion University, Norfolk, VA 23529, Report 849, 33 p.

[7] U.S. Department of Commerce, National Ocean Service, NOAA, Ocean and Lake Level Division Database, Rockville, MD 20874, June 1992.

Standard length and otolith maximum diameter (OMD) relation

We found that in wild-caught larval Atlantic croaker, faster-growing individuals have larger otoliths than similar-size slower-growing individuals. Our results differ from results found for laboratory-reared guppies (*Poecilia reticulata*) (Reznick et al., 1989), pond-reared striped bass (*Morone saxatilis*) (Secor and Dean, 1989), red seabream (*Pagrus major*), and spot (*Leiostomus xanthurus*) (Secor et al., 1989). In these studies, where food ration was controlled, slower-growing individuals had larger otoliths than similar-size faster-growing individuals. However, in Arctic char (*Salvelinus alpinus*), otolith growth rate has been found to continue increasing while somatic growth remains constant when exposed to temperatures above 13°C (Mosegaard et al., 1988). In our study, the early-captured, faster-growing Atlantic croaker, may have experienced otolith growth that exceeded their maximum somatic growth rate.

Unfortunately, there are no quantitative data that can be tested to determine what factors influenced the growth of Atlantic croaker in our samples and what were the subsequent effects on the otolith growth-somatic growth relation. The underlying issue, however, is to examine how the fish and otolith-size relation is affected by temperature responses of somatic growth rate at particular food levels (Mosegaard et al., 1988) and to determine its significance when backcalculating growth from increment widths (Campana and Jones, 1992).

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Temporal and spatial spawning patterns of the Atlantic butterfish, *Peprilus triacanthus*, in the South and Middle Atlantic Bights*

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Abstract.—Three species of the stromateoid genus *Peprilus* have been found to occur in the northwest Atlantic: *P. triacanthus* (butterfish), *P. burti* (gulf butterfish), *and P. alepidotus* (harvestfish). *Peprilus triacanthus* and *P. alepidotus* reportedly spawn from May through August and June through July, respectively. *Peprilus burti* spawns twice yearly: February through May and September through November. Collections of larvae and juveniles of *Peprilus* spp. from the northern South Atlantic (SAB) and Mid-Atlantic (MAB) Bights during both the spring and summer of 1988 and 1989 suggest that either a combination of species was spawning or that reported spawning dates were suspect. Species identification of *Peprilus* in these collections was determined with morphometric, meristic, and pigment character analyses. Specimens sampled had counts for caudal vertebrae (18–19) and ventral midline melanophores (11–16) consistent with those found for *P. triacanthus* in previous studies. By analyzing otoliths, we estimated larval and juvenile growth rates to be approximately 0.23 mm/day. Backcalculation of hatch dates suggests either two spawning events for *P. triacanthus*, February through mid-April and mid-May through late July, or one extended spawning period beginning in late February and ending in late July. This study reveals that *P. triacanthus* spawns for a much longer period than previously thought. It is possible that *P. triacanthus* spawns during the spring in the SAB and summer in the MAB as a strategy to extend the duration of its spawning period. This strategy is one used by other north-south migrating species and warrants further study.

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Three species of the stromateoid genus *Peprilus* (order: Perciformes) are reported to occur in the western North Atlantic: butterfish, *P. triacanthus* (Peck), gulf butterfish, *P. burti* (Fowler), and harvestfish, *P. alepidotus* (Linnaeus). Although the ranges of all three species extend along the eastern coast of North America and the West Indies, there is some question as to which species of *Peprilus* are regular residents in the South Atlantic Bight (SAB) and Mid-Atlantic Bight (MAB) regions (Caldwell, 1961; Haedrich, 1967; Horn, 1970; Perschbacher et al., 1979). This question is extended by the suggestion of possible hybridization between *P. triacanthus* and *P. burti* in the northern portion of the SAB (Horn, 1970; Perschbacher et al., 1979).

Reproduction in *P. triacanthus* and *P. burti* is seasonal and apparently associated with annual migration patterns (Horn, 1970). In the summer and fall, *P. triacanthus* migrates northward and inshore, where it reportedly spawns from late May through August, with a peak in June (Horn, 1970). During winter, *P. triacanthus* migrates offshore and becomes horizontally restricted (Horn, 1970). Movement by *P. burti* is somewhat opposite to that of *P. triacanthus*. *Peprilus burti* migrates offshore during late spring through early fall, then onshore towards shallow bays and inlets during the winter and early spring (Horn, 1970). Spawning by *P. burti* is reported to occur during two distinct periods, February through May and September through November (Murphy, 1981). Unlike these other two species, *P. alepidotus* does not exhibit seasonal migration patterns, remaining in shallow waters throughout the year where it spawns during June and July (Horn, 1970).

During the spring and summer seasons of 1988 and 1989, we consistently collected larval and juvenile *Peprilus* from the South Atlantic and Mid-Atlantic Bights. The combination of their location and dates of capture raised the question as to which species were present in our samples. Although most abundant within the MAB region, *P. triacanthus* is reported to spawn during the summer only (Horn, 1970). According to time of capture, the spring-collected larvae in our SAB samples should have been *P. burti* because they were collected before *P. triacanthus* and *P. alepidotus* supposedly begin to spawn (Horn, 1970; Murphy, 1981). However, their occurrence within the South Atlantic and Mid-Atlantic Bights suggests that they were either *P. alepidotus* or *P. triacanthus*. Thus, the overall aim of this study was to identify the species in our samples and to back-

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calculate hatching dates by using validated otolith-increment analysis.

Materials and methods

Collections

Peprilus larvae and juveniles were collected during April and May of 1988 and April of 1989 in the northern SAB, offshore of Cape Hatteras, North Carolina, and June–August of 1988 and 1989 in the MAB, from Long Island, New York, to Cape May, New Jersey (Fig. 1; Table 1).

Fish were collected with a 1-m^2 Tucker trawl and a 5-m^2 Frame trawl. The Tucker trawl had three opening-closing 505-µm mesh nets. Five-minute tows were taken at three primary depth intervals: 0–5 m, 5–10 m, and 10–15 m. For the purpose of this study, all depths were combined. The Frame trawl was fitted with a 2-mm mesh net and towed at the surface for 10 minutes. A flowmeter was attached to each net to estimate the volume of water sampled.

Tucker trawl samples were split in half with a Folsom plankton splitter. One half of each sample was preserved in 5% buffered formaldehyde and used for identification and length and body depth measurements. The other half was preserved in 95% ethanol and used for otolith analysis. Frame samples were preserved in 95% ethanol. Samples were sorted in the laboratory with a dissecting microscope for eggs, larvae, and juveniles.

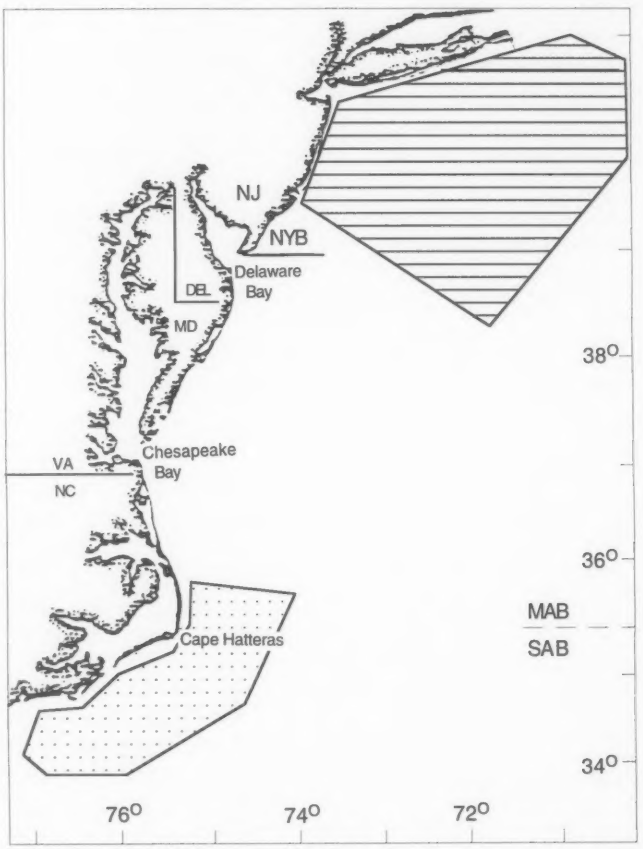

Figure 1

Study area from Cape Hatteras, North Carolina, to Long Island, New York. Dotted and barred areas represent spring and summer sampling areas, respectively.

Morphometrics

Determination of a seasonal difference in body size was accomplished by analyzing body depth (BD) and standard length (SL) for all specimens collected. Measurements were made to the nearest 0.1 mm with either a video-enhanced digitizing system (Optical Pattern Recognition System, BIOSONICS, Inc.) or an ocular micrometer. Standard length was measured from tip of the snout to the tip of notochord. Body depth was measured perpendicular to the longitudinal body axis at the anterior margin of the pectoral base (Ditty, 1981).

To examine differences in body depth between spring and summer seasons, linear regressions of body depth on standard length were calculated for Tucker and Frame cruises, 1988 and 1989. Slopes of regression lines were tested for homogeneity. Allometric effects of growth on body depth were examined by calculating regressions of body depth on standard length as a function of standard length.

Meristics

To determine the species composition of the spring- and summer-collected *Peprilus* larvae, two meristic characters were examined: number of caudal vertebrae and number of ventral midline melanophores. Character counts were compared with published data for each of the three possible species (caudal vertebrae: Ditty, 1981; ventral midline melanophores: Ditty and Truesdale, 1983). Subsamples of specimens were either cleared and stained (Taylor, 1967; Wassersug, 1976; Dingerkus and Uhler, 1977; Potthoff, 1984) or x-rayed (Gosline, 1948; Miller and Tucker, 1979; Tucker and LaRoche 1984; Kosenko et al., 1987). Photomicrographs of cleared and stained specimens were taken and slides developed for further

Table 1

List of 1988 and 1989 cruises, sampling dates, number of fish collected, and locations. SAB = South Atlantic Bight; MAB = Mid-Atlantic Bight.

Net	Cruise	Date	No. of fish captured	Location
1988	DEL88-5-2	24 April–1 May	71	SAB
Frame	ATLANTIC TWIN	21 May–23 May	29	SAB
	DEL88-7-1	1 June–3 June	3	MAB
	DEL88-7-2	11 June–16 June	22	MAB
	DEL88-7-3	6 July–9 July	4	MAB
	DEL88-7-4	16 July–22 July	99	MAB
	DEL88-7-5	29 July–2 August	50	MAB
	DEL88-7-6	8 August–12 August	110	MAB
Tucker	DEL88-7-3	6 July–9 July	188	MAB
	DEL88-7-4	16 July–22 July	1,191	MAB
	DEL88-7-5	29 July–2 August	514	MAB
	DEL88-7-6	8 August–12 August	1,063	MAB
1989				
Frame	FE1-89	25 April–29 April	158	SAB
	ONR1-89	30 May–2 June	8	MAB
	ONR2-89	6 June–7 June	4	MAB
	FE2-89	7 July–10 July	2	MAB
	ONR4-89	18 July–2 August	22	MAB
	ONR5-89	14 August–18 August	170	MAB
Tucker	FE1-89	25 April–29 April	201	SAB
	FE2-89	7 July–10 July	445	MAB
	ONR4-89	18 July–2 August	89	MAB
	ONR5-89	14 August–18 August	146	MAB

inspection. Fish were x-rayed with a Kodak Faxitron at settings of 40 kilovolts, 20 milli-amperes and 30 seconds, which gave the best results with Kodak Industry X negatives. These negatives were placed in a Kodak GBX developer and replenisher solution for 2 to 3 minutes, rinsed in water, placed in a Kodak GBX fixer solution for 5 minutes, rinsed for 15 minutes in water, and dried overnight. Caudal vertebrae were counted with the aid of a dissecting scope and included those vertebrae attached to the first fully formed hemal spine and extending to the urostyle (Gosline, 1960).

Caudal vertebrae counts were made for larvae selected to cover the range of sizes (all were larger than 7 mm, the size at which Ditty (1981) found most fish to have adult characters), body depth-standard length ratios (shallow and deep-bodied), and dates of capture (spring and summer) encountered. Caudal vertebrae were counted for a subsample of 34 cleared-and-stained fish and 64 x-rayed fish from the 1988 Frame trawls and 76 x-rayed fish from the 1989 Frame trawls.

Ventral midline melanophores were counted for a subsample of 50 fish (25 from the spring and 25 from the summer) smaller than 4 mm SL (the size at which Ditty based his observations). These fish were randomly chosen from 1989 formalin-preserved collections. Ventral midline melanophores were considered to be those located between the hindgut and notochord tip (Ditty, 1981).

Otolith marking experiment

Otoliths of 22 fish were marked with oxytetracycline hydrochloride (OTC) in August of 1991 to determine if *Peprilus* larvae and juveniles deposit daily rings. Sizes of fish ranged from 10 to 31 mm SL. Fish were acclimated for two days in a five-gallon bucket with built-in screening that allowed water to flow-through the bucket when it was placed in an aerated seawater bath. Fish were fed twice daily with either live *Artemia* nauplii or live field-captured zooplankton during both acclimation and experimental periods. Experimental conditions were maintained as follows: temperature fluctuated between 12°C and 24°C, salinity ranged from 28 to 30‰, pH varied from 7.6 to 8.0 (however, during marking the pH dropped to 6.5 and 6.6), and the photoperiod remained constant at a 14-h light and 10-h dark cycle.

The marking procedure followed those for mass-marking larvae and juveniles (Hettler, 1984; Tsukamoto, 1985; Muth et al., 1988). Briefly, fish were immersed in a 450 mg/L concentration of OTC for a six-hour period. Fish were covered during the marking period to decrease the amount of light because light may interfere with the effectiveness of tetracycline (Secor et al.[1]). While immersed in the marking solution, four fish died. The remaining 18 fish were transferred from the marking solution and placed inside

two five-gallon screened buckets. Two additional fish died during the transfer process. Fifteen of the remaining 16 fish survived until the end of the experiment. At four days after marking, four fish were sacrificed. An additional four fish were sacrificed five days after marking. Three fish were sacrificed eight days after marking.

To add a second mark, the remaining four fish were immersed a second time (12 days after the initial marking) and were fed amphipods and brine shrimp that had been immersed in a 450mg/L OTC seawater solution for five hours. These fish were held and fed in a fresh 450 mg/L concentration of OTC for 16 hours. Ten days after the second immersion the remaining four fish were sacrificed.

All specimens were placed in 95% ethanol for preservation. Otoliths were dissected from fish and placed in immersion oil on glass slides. Otoliths were ground with a size-600 carborundem grit and mineral oil slurry. The tetracycline mark was viewed under a Zeiss ultraviolet microscope with a Zeiss FITC acridine-orange excitation filter set. Increments were counted blindly by one reader, a minimum of three times. If the number of increments between counts differed by more than one, the otolith was not used. The number of increments present after the mark was regressed against the number of days since marking; the regression coefficient was compared with unity by using a t-test.

Otolith ageing

Otolith ageing was performed to determine a length-age relationship for our combined *Peprilus* spp. samples. The presence of daily increments in temperate and tropical water fishes has been noted by Pannella (1971, 1974). Fish fixed and preserved in 95% ethanol and ranging in size from 6 to 28 mm SL were aged from 1988 spring (n=30) and summer (n=33) samples to determine seasonal growth rates. Sagittae and lapilli were removed from each fish following the techniques of Brothers (1984). Otoliths were placed in type-B immersion oil and left to clear for one month. Sagittae were analyzed with a video-enhanced digitizing system (Optical Pattern Recognition System) viewed at 250× with an oil immersion lens.

Increments were counted blindly by one reader a minimum of two times. If counts differed between readings by more than three increments, they were not used. Counts were made along the longest radial axis whenever possible (Brothers, 1980). When otoliths were too thick to see increments clearly, they were ground with size-600 carborundem grit and immersion oil to create thinner sections (Brothers, 1980).

A length-at-age relationship was determined by regressing standard length on age. Because most fish deposit increments on their otoliths either at hatching or yolk-sac absorption (Brothers et al., 1976), a y-intercept of hatch size (1.72 mm; Colton and Honey, 1963) was assigned to the regression. The slope of the spring regression, i.e. growth rate, was compared with the slope of the summer regression by means of a homogeneity of slopes test. To determine date of hatching, an age-on-length relation was first determined. The y-intercept for this equation was determined by the best fit of the data. This regression equation was solved for age by using standard lengths of all 1988 and 1989 Tucker- and Frame-caught fish (size range of 6.0–28.0 mm SL). Hatching dates were backcalculated by subtracting age at capture from the capture date. Hatching date distributions were then plotted to determine spawning date distributions for all 1988 and 1989 Frame-trawl–caught and Tucker-trawl–caught butterfish.

Results

Collection

During 1988, 3,980 *Peprilus* were collected in the Tucker trawl (4 cruises; 196 hauls), and 388 in the Frame trawl (8 cruises; 404 hauls). In 1989, 880 Tucker-trawl–caught (4 cruises; 128 hauls) and 364 Frame-trawl–caught (6 cruises; 158 hauls) *Peprilus* were collected. In 1988, the greatest number of larvae and juveniles were caught in Tucker trawls in the MAB, July (n=1,191; 24.3 per haul) through mid-August (n=1063; 21.7 per haul). There were no Tucker trawl collections during the spring of 1988 in the SAB. The highest numbers of *Peprilus* were collected in 1989 cruises from mid-July through early August in the MAB (n=445; 17.8 per haul). In general, the number of fish collected in the Frame trawl was less than in the Tucker trawl. In the 1988 Frame trawls, *Peprilus* were most numerous during late May (n=29; 1.8 per haul) in the SAB and from mid-July (n=99; 2.0 per haul) through mid-August (n=110; 2.2 per haul) in the MAB. Frame trawls for 1989 had the greatest abundances of larvae during late April (n=158; 4.3 per haul) in the SAB and from mid-July through early August in the MAB (n=170; 4.4 per haul).

[1] Secor, D. H., E. D. Houde, and D. M. Monteleone. 1995. Development of otolith-marking methods to estimate survival and growth of early life stages of natural and hatchery-produced striped bass in the Patuxent River in 1991. Maryland Department of Natural Resources, Chesapeake Bay Research and Monitoring Division, CBRM-GRF-94-1, 145 p.

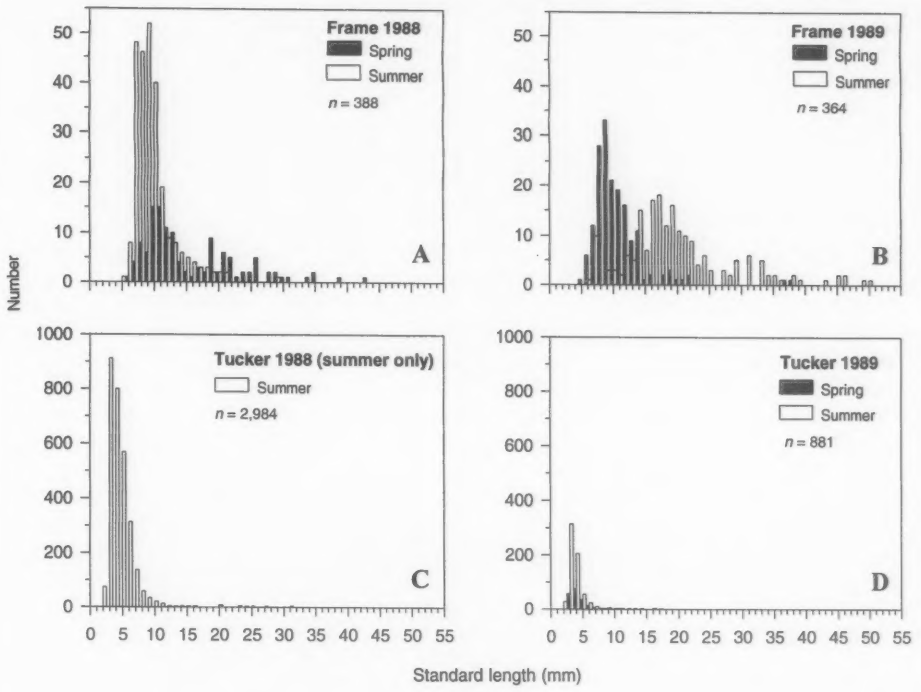

Figure 2

Length-frequency histograms for *Peprilus triacanthus* collected by net during the spring and summer of 1988 and 1989.

Morphometrics

A wide range of sizes of *Peprilus* were collected during both seasons of 1988 and 1989. Because size-frequency distributions had the same mode on all cruises within a season, length frequencies were combined for all fish sampled with a particular gear during each season each year. Spring-collected 1988 fish ranged in size from 6 to 43 mm SL (Frame; Fig. 2A). Similar size distributions of fish were found for the 1989 spring cruises: 4.7 to 37.5 mm SL (Frame; Fig. 2B) and 2 to 6 mm SL (Tucker; Fig. 2D). The 1988 summer trawls collected fish between 5 and 29 mm SL (Frame; Fig. 2A) and 1.3 to 36.0 mm SL (Tucker; Fig. 2C). Summer 1989 fish ranged in size from 6.0 to 50.0 mm SL (Frame; Fig. 2B) and 1.7 to 49.0 mm SL (Tucker; Fig. 2D).

Deep- and shallow-bodied fish were identified from both the spring and summer samples in both years. Fish had BD-SL ratios ranging from 0.119 to 0.750 (Fig. 3, A and B). There was an indication of two modes during both spring and summer of 1989. These BD:SL ranges overlap with ranges reported by Horn (1970) and Ditty (1981) for all species (Table 2). Further analysis of body depth: standard length demonstrated that body depth increases allometrically with respect to standard length up to a size of 10 to 15 mm SL (Fig. 4). Body depth subsequently remained about 50% of length for each year.

Meristics

Ninety-nine percent of the fish collected with the Frame net in 1988 and 1989 had either 18 or 19 caudal vertebrae (of those, approximately 90% had 19 caudal vertebrae; Table 3). Counts of either 18 or 19 caudal vertebrae are consistent with those reported for *P. triacanthus* (Table 3). The number of caudal vertebrae was not related to body depth. According to Ditty and Truesdale (1983), juvenile *P. burti* and *P. alepidotus* have mean body depth-standard length ratios of greater than 0.557 and caudal vertebrae counts of 17–18. However, our findings indicate that fish with high body depth-standard length ratios also had 19 caudal vertebrae.

The fish we sampled had between 8 and 16 ventral midline melanophores. Ditty (1981) reported ranges of 4 to 8 ventral midline melanophores for *P. burti* and 11 to 17 for *P. triacanthus*. Seventy-six percent of our speci-

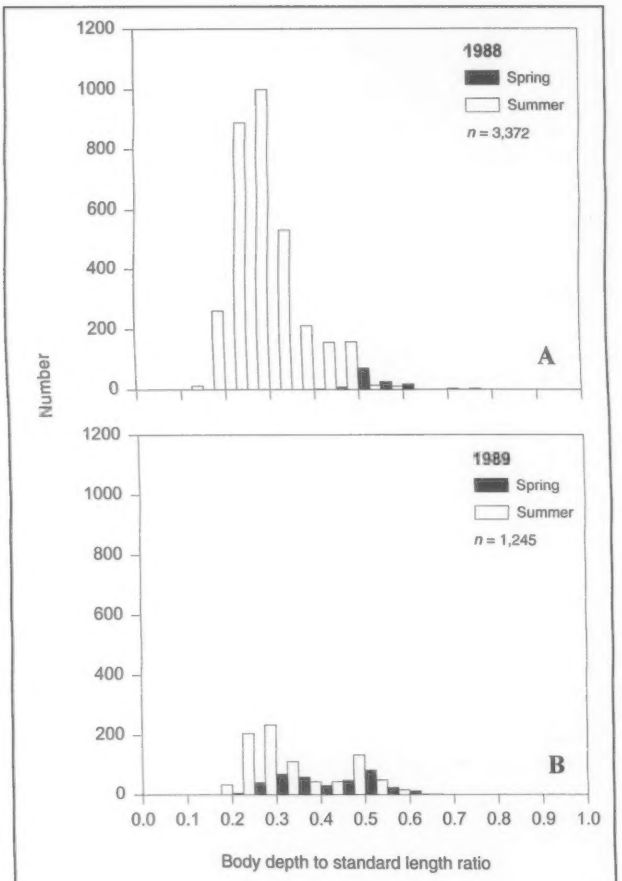

Figure 3

Body depth to standard length-frequency histograms for *Peprilus triacanthus* collected during the spring and summer of 1988 and 1989. Frame- and Tucker-trawl collections were combined.

mens sampled had 11 to 17 ventral midline melanophores, and 94% had 10 to 16 melanophores. These data suggest the presence of *P. triacanthus* in our samples. On further analysis of pigment patterns, we found no difference among specimens (Rotunno, 1992). These data corroborate our caudal vertebral counts.

Otolith marking experiment

Daily increment formation was a valid indicator of age of *Peprilus* spp.. The presence of subdaily increments was also noted in these otoliths. The number of increments observed after the tetracycline mark regressed against the number of days since marking showed a 1:1 correspondence (Fig. 5). A y-intercept value of zero was assigned to the regression. The slope of the regression (0.921) did not differ significantly from unity (t-test: t=0.82, P=0.42).

Growth and hatching date

Spring and summer growth rates were estimated from 1988 collections of *Peprilus* at 0.233 mm/day and 0.219 mm/day, respectively. These growth rates were not significantly different (F=2.071, P=0.155). Therefore, seasons were combined and an overall regression was computed that yielded an average growth rate of 0.225 mm/day (Fig. 6). The regression equation ($Age = 3.433(SL) + 8.270$, r^2=0.93) was used to backcalculate hatching dates from length frequencies. This age-length relation was also applied to 1989 collections for back-calculation purposes.

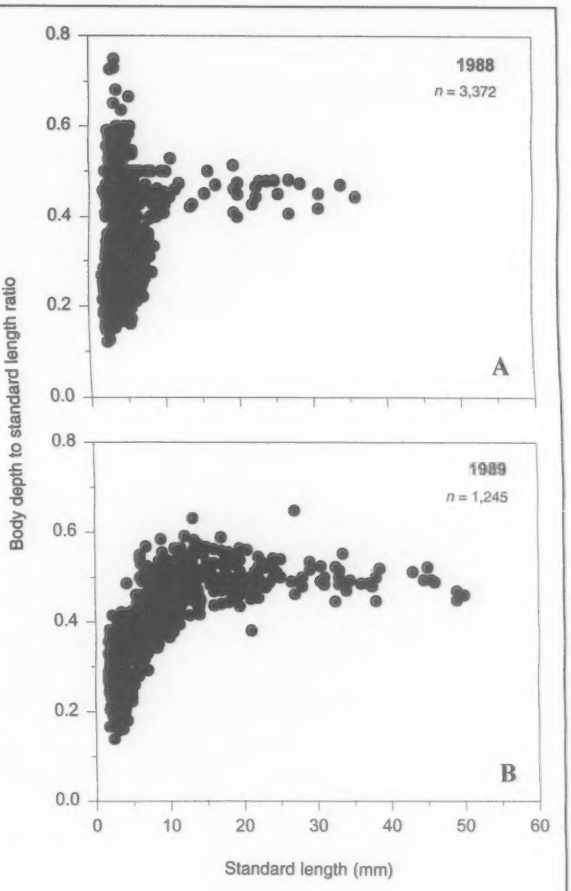

Figure 4

Body depth to standard length versus standard length for *Peprilus triacanthus* collected during the spring and summer of 1988 and 1989. Frame- and Tucker-trawl collections were combined.

Hatching for *P. triacanthus* in our samples occurs from February through at least July and appears to be concentrated in two peaks that occur during early spring and summer (Fig. 7, A and B). The earliest hatching date recorded for fish caught in 1988 was 19 January 1988 and the latest was 22 July 1988. The winter-spring spawning appears to begin in January and continue through late April, with an apparent peak in March in the SAB (Fig. 7A). A decrease in spawning occurs at this time, although some spawning continues at a low level through May (Fig. 7A). Spring-summer spawning occurs during June and July in the MAB with a peak in late June. The relative strength of these two spawnings is not clear because sampling effort was not equivalent during each season.

Fish caught in 1989 had a similar spawning pattern to that of fish collected in 1988; the earliest hatching date calculated was 14 February 1989, the latest was 29 July 1989 (Fig. 7B). Spawning peaks occurred in late March to early April in the SAB and early to mid-June in the MAB. There appears to be a reduction in spawning during the month of May along the U.S. Atlantic coast.

Discussion

Peprilus triacanthus is the most common species of *Peprilus* found along the Atlantic coast of the United States. Within the New York Bight, spawning and larval presence for *P. triacanthus* is reported to oc-

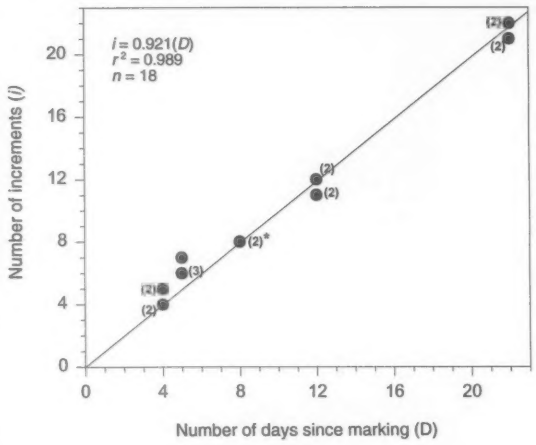

Figure 5

Number of increments observed after oxytetracycline hydrochloride mark versus the number of days since marking for a subsample of 1988 Frame-caught *Peprilus triacanthus*. Numbers in parentheses represent the number of fish. *n = 3, but one otolith was not readable.

Table 2

Body depth-standard length ratios reported by Horn (1970), Ditty and Truesdale (1983), and from our Frame and Tucker trawl surveys.

	Body depth-standard length range	Standard length range (mm)	*n*
Horn (1970)			
P. burti	0.460–0.640	7.80–167.00	232
P. triacanthus	0.364–0.600	10.60–198.00	202
P. alepidotus	0.565–0.877	18.22–222.00	205
Ditty (1981)			
P. burti	0.241–0.579	2.16–19.82	160
P. triacanthus	0.235–0.546	2.04–20.86	159
P. alepidotus	0.205–0.750	1.85–18.92	80
1988 and 1989 Frame and Tucker			
Spring	0.187–0.750	2.01–43.00	496
Summer	0.119–0.727	1.29–50.00	4,121
Spring and Summer	0.119–0.750	1.29–50.00	4,617

cur during summer only (Wilk et al., 1990). Fahay (1975) suggested however, on the basis of the range of larval lengths collected in 1967–68, that spawning of *P. triacanthus* may occur throughout the year in the SAB. The occurrence of larval and pelagic juvenile *Peprilus* within our spring samples collected in the northern SAB suggests two possible scenarios: 1) a species other than the most commonly found *P. triacanthus* spawns within the Atlantic (e.g. *P. burti*) or 2) *P. triacanthus* or *P. alepidotus* has a more protracted spawning season than previously thought. *Peprilus* larvae and juveniles in our samples proved to be *P. triacanthus*; therefore, our results demonstrate an extended spawning period for *P. triacanthus*

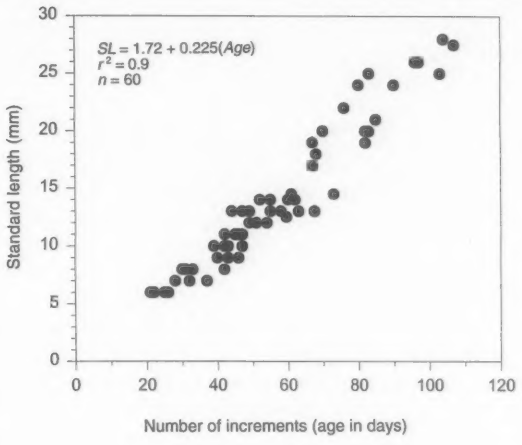

Figure 6

Standard length versus the number of increments for a subsample of 1988 Frame-caught *Peprilus triacanthus*.

Table 3

Vertebral counts for *Peprilus* collected by Collette (1963), Horn (1970), Ditty (1981), and in this study (Frame).

	Standard length (mm) range	16	17	17–18	18	18–19	19	20	*n*
Collette (1963)									
P. burti	—	2	92	0	2	0	0	0	96
P. triacanthus	—	0	4	0	36	0	138	2	180
Horn (1970)									
P. burti	6.0–115.0	5	262	0	6	0	0	0	273
P. triacanthus	6.0–115.0	0	7	0	62	0	208	2	279
P. alepidotus	6.0–115.0	3	176	0	3	0	0	0	182
Ditty (1981)									
P. burti	7.14–14.45	0	13	9	0	0	0	0	22
P. triacanthus	7.14–14.73	0	0	0	1	8	10	0	19
P. alepidotus	7.74–11.01	0	5	0	0	0	0	0	5
Frame									
Spring 1988	8.0–26.0	0	0	0	4	0	48	0	52
Summer 1988	8.0–26.0	0	1	0	6	0	39	0	46
Spring 1989	8.52–37.5	0	0	0	2	0	28	0	30
Summer 1989	8.0–38.0	0	0	0	6	0	39	1	46
Total Frame	8.0–38.0	0	1	0	18	0	154	1	174

in the Atlantic. According to back-calculated hatching dates, *P. triacanthus* spawns from late January through at least July. We did not observe any seasonal differences in body depth. However, geographic differences in body depth need to be further analyzed before discounting the existence of either a polymorphic *P. triacanthus* or a hybrid of *P. triacanthus* and *P. burti*.

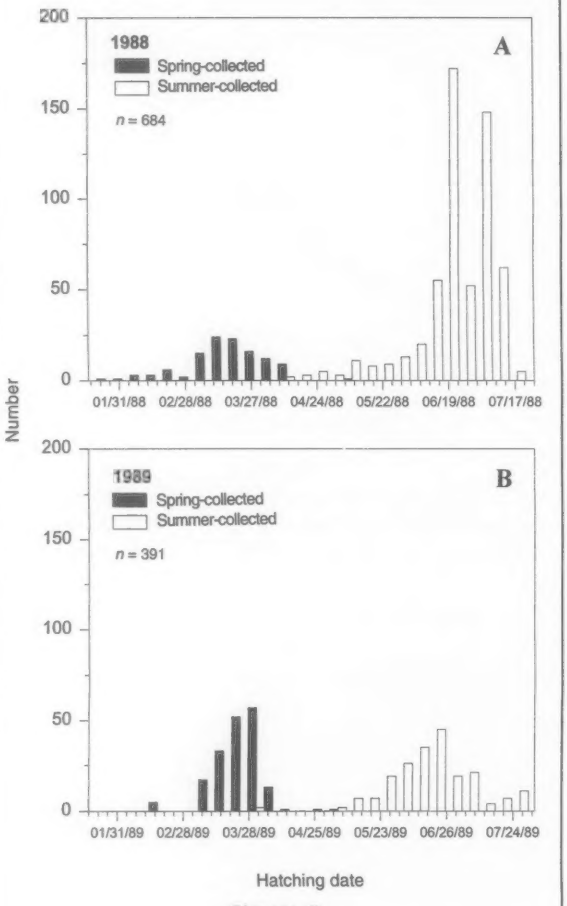

Figure 7

Back-calculated birthdate distributions for all spring and summer samples collected during 1988 and 1989. Frame- and Tucker-trawl samples were combined.

Species identification

According to the reported ranges of body depth-standard length ratios (Horn, 1970; Ditty and Truesdale, 1983), our larval specimens could have been any one of the Atlantic or Gulf coast species of *Peprilus*. However, two points must be considered when interpreting these data. First, we found a strong allometric relation between body depth and standard length for individuals smaller than 15 mm SL. Because the collections of Horn (1970) include fish ranging in size from 6 to 222 mm SL, this allometric relation could have confounded his conclusions. Ditty and Truesdale (1983), however, apparently recognized this problem and therefore presented their data by size class. Second, our other analyses (caudal vertebrae and melanophore counts) supported the contention that *P. triacanthus* was the dominant species of *Peprilus* in our samples. Our sample was predominantly composed of individuals with 19 caudal vertebrae, which was consistent with findings of previous authors for *P. triacanthus* (Collette, 1963; Horn, 1970; Ditty and Truesdale, 1983). The ventral midline melanophore counts were also similar to those used for *P. triacanthus* by Ditty (1981).

The overall results of the above morphometric, meristic, and pigment analyses lead us to conclude that *P. triacanthus* is the dominant and probably the only species of *Peprilus* collected in our samples. The two most definitive characters for identification were

the number of caudal vertebrae and ventral midline melanophores.

Age and growth

Ages of larval and juvenile *P. triacanthus* can be determined by counting otolith increments. Validation was necessary because of the prevalence of subdaily increments in this species. Secondary nuclei (multinucleation) were also noted in *Peprilus otoliths*. The cause and timing of the formation of secondary nuclei are not presently understood (Campana and Neilson, 1985), although these secondary nuclei have been demonstrated to form during metamorphosis in bluefish (Hare and Cowen, 1994). Secondary nuclei, in butterfish otoliths, do not seem to follow a consistent pattern in the development of the fish; we found that two sagittal bones from one fish frequently contained differing numbers of secondary nuclei. Although secondary nuclei may form during metamorphosis (Campana and Neilson, 1985; Hare and Cowen, 1994), we found secondary nuclei in larvae that were several millimeters smaller than the size at which metamorphosis occurs (16 mm).

Larval and early juvenile *P. triacanthus* from 6.0 to 28.0 mm SL grew at a rate of 0.227 mm/day. Although ages of young butterfish have not been recorded previously, Colton and Honey (1963) gave sizes of *P. triacanthus* from hatching to six days of age. Based on their estimates, growth rates ranged from 0.01 to 0.55 mm/day and decreased with the age of the fish. Specimens of young *P. burti* have been aged with modal length-frequency analysis; growth rates of *P. burti* ranged from 0.25 to 0.56 mm/day (Murphy and Chittenden, 1990). *Peprilus burti* may be expected to have a higher growth rate than *P. triacanthus* owing to the fact that it spawns in warmer waters of the Gulf of Mexico.

Our analysis of hatching-date distributions demonstrated that *P. triacanthus* has a more extensive spawning season than previously reported. Their spawning effort seems to be focused into two cohorts (spring: February–March; and summer: June–July) although evidence is presented that suggests at least some fish spawn during the interim period between seasonal peaks (i.e. late April to early June). Kawahara[2] speculated that *P. triacanthus* may begin spawning in April. It should be noted that Kawahara (1977) based his spawning estimate on adult growth rates, which are higher than our estimate for larvae and juveniles and, therefore, would have underestimated the spawning duration.

A bimodal hatching-date distribution in *P. triacanthus* is similar to that reported for another north-south migrating species within the western Atlantic, the bluefish, *Pomatomus saltatrix* (Kendall and Walford, 1979; Nyman and Conover, 1988). However, Hare and Cowen (1993) and Smith et al. (1994) have proposed that *P. saltatrix* spawns continually during its north-south migration and that the apparent bimodal hatching date distribution may result from advective processes acting on the larval distributions and from sampling artifact.

The presence of an apparent bimodal spawning in *P. triacanthus*, with spring and summer peaks, may be an artifact of our sampling. Because we did not sample from April to June in each year and because our sampling locations were spatially distinct between spring and summer, it is possible that we did not collect larvae spawned during May and early June. However, we could have collected older fish in our samples that were spawned early in June. Data collected monthly by the National Marine Fisheries Services (NMFS) as part of their Monitoring, Assessment, and Prediction (MARMAP) surveys suggest that larvae are indeed present from April to August in the MAB, thus it is likely that spawning occurs continually (Fig. 8). Moreover, MARMAP data indicate a northward progression of larvae from near Cape Hatteras during March or April (or both) into the entire MAB by mid-summer and until October. This spatio-temporal pattern is consistent with the possibility of spawning associated with a seasonal northward migration of adult *P. triacanthus*. Horn (1970) has speculated that butterfish movements are highly influenced by temperature (and salinity to a lesser degree). Temperature-related movements by butterfish (and bluefish) would correspond with the observed northward progression of young larvae from the SAB in the spring into the MAB in the summer in association with seasonal warming. The extent of north-south migration by *P. triacanthus*, however, requires further study.

In conclusion, this study adds to our current knowledge of the early life history and spawning seasonality of butterfish, *P. triacanthus*. Our finding of a more protracted spawning season and of a seasonal difference between spawning locations should be of value in reassessing management plans for this species. Current management plans are based on conclusions that *P. triacanthus* spawns during summer months only. The apparent similarity of spawning periodicity of butterfish to that of bluefish (Cowen et al., 1993; Hare and Cowen, 1994, Smith et al., 1994) suggests

[2] Kawahara, S. 1977. Age and growth of butterfish, *Peprilus triacanthus* (Peck), in ICNAF Subarea 5 and Statistical Area 6. ICNAF Res. Doc. 77/VI/27. June 1977 Annual Meeting. Far Seas Fishery Laboratory, Shimizu, Japan.

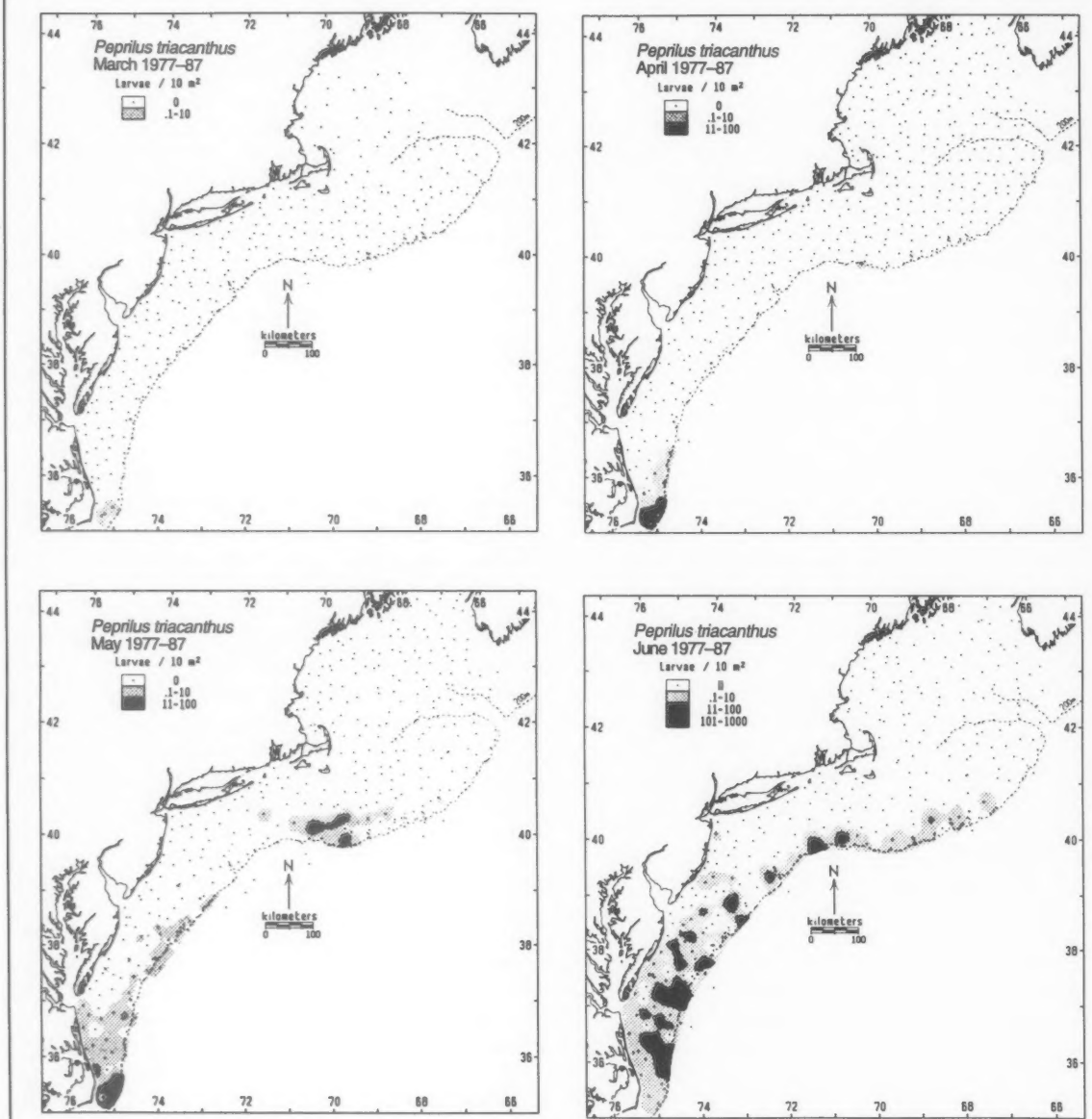

Figure 8

MARMAP monthly averaged collections (March through October) of larval *Peprilus triacanthus* during the years (1977–87).

that a possible adaptive strategy may be shared by these two seasonally migrating pelagic species. Perhaps with closer inspection, other seasonally migrating species may be found that share this spawning strategy (Hare and Cowen, 1996). Further study into the basis of this pattern is warranted.

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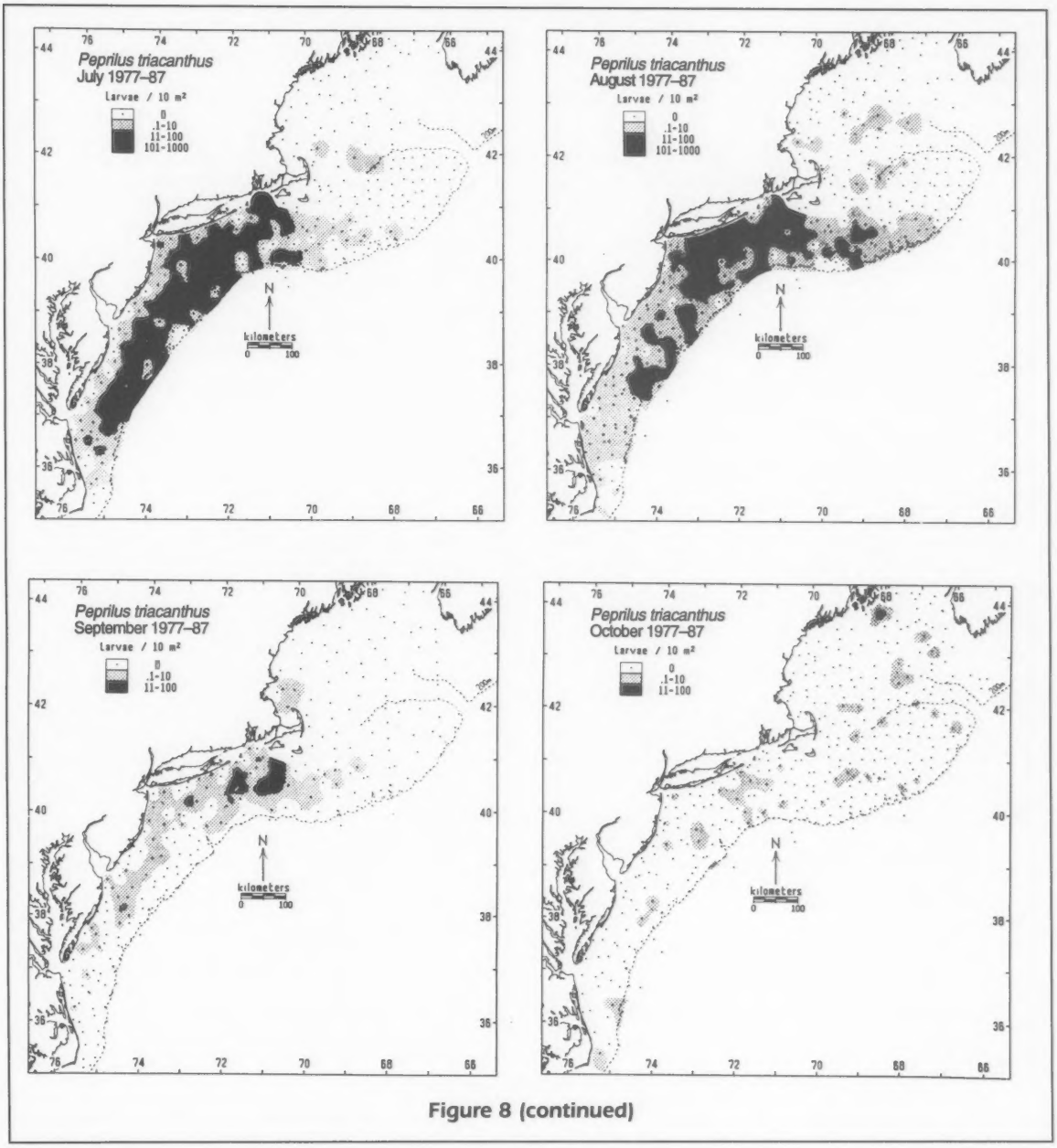

Figure 8 (continued)

and two anonymous reviewers. Jon Hare provided help with all phases of larval identification and otolith analysis. Mike Fahay generously provided Figure 8. This work is a result of research sponsored by the NOAA Office of Sea Grant, U.S. Department of Commerce, under Grants #NA86AA-D-SG045 and #NA90AA-D-SG078 to the New York Sea Grant Institute.

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A comparison of three genetic methods used for stock discrimination of orange roughy, *Hoplostethus atlanticus*: allozymes, mitochondrial DNA, and random amplified polymorphic DNA

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Abstract.—Three types of genetic markers were used to determine genetic relations among four spawning populations of orange roughy off New Zealand. Eleven allozyme loci were tested in starch and cellulose acetate gels. Restriction fragment length polymorphisms were tested in two regions of the mitochondrial DNA amplified with the polymerase chain reaction. Random amplified polymorphic DNA (RAPD) products were generated with 10-base oligonucleotide primers and separated in agarose gels. There was a significant heterogeneity among all four populations, at 5 out of 11 allozyme loci, at 2 of 29 RAPD primer fragments, and in the frequency of mtDNA haplotypes. There was no significant difference between the two northern spawning populations for any marker, but there were significant differences between all other pairwise population comparisons with allozymes and RAPD's, indicating the presence of three genetic stocks. The mtDNA analysis revealed less genetic subdivision than did allozymes and RAPD's.

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Fishery Bulletin 95:800–811 (1997).

The orange roughy, *Hoplostethus atlanticus*, is a deepwater species with wide distribution in the Atlantic, Indian, and South Pacific Oceans. Around New Zealand the species supports a fishery which peaked at 50,000 tons per annum in the mid 1980's but which has subsequently declined owing to quota restrictions. There are several geographically isolated spawning populations of orange roughy which are the major targets of fishing within the New Zealand Exclusive Economic Zone (EEZ).

A basic prerequisite of fisheries management is the identification of production units or stocks of a species; inadequate knowledge of stock structure may lead to over- or under-exploitation. Orange roughy occur at depths of about 1,000 m and therefore tag and release studies to estimate movements between areas are impracticable. There have been several other approaches to stock identification of orange roughy with differing results. Studies of parasite distribution (Lester et al., 1988), morphometric characters (Linkowski and Liwoch, 1986; Haddon and Willis, 1995), and trace element composition of otoliths (Edmonds et al., 1991) have demonstrated regional subdivisions in Australasian orange roughy. An allozyme study revealed a high level of genetic variation but only marginally significant differences between the fishing areas around New Zealand (Smith, 1986). Genetic evidence for discrete stocks off South Australia and eastern Australia based on an allozyme survey (Black and Dixon[1]) was not supported by a larger-scale study (Elliott and Ward, 1992). Restriction fragment length polymorphism (RFLP) analyses of mitochondrial (mt)DNA have indicated genetic subdivision of orange roughy around Australia (Smolenski et al., 1993) and New Zealand (Smith et al., 1996).

The development of the polymerase chain reaction (PCR), which amplifies DNA, enables genetic analyses to be carried out on small tissue samples and provides a range of methods for the population biolo-

[1] Black, M., and P. I. Dixon. 1989. Population structure of orange roughy (*Hoplostethus atlanticus*) in Australian waters. Internal Report, Centre for Marine Science, University of New South Wales, Kensington, Australia, 22 p.

gist without need for cloning and sequencing. PCR amplification of specific regions of mtDNA and digestion with restriction enzymes (PCR-RFLP) has been used as a fisheries tool for the differentiation of various fish species (Chow et al., 1993; Chow and Inoue, 1993) and for stock identification of albacore tuna (Chow and Ushiama, 1995), anchovies (Bembo et al., 1995), and salmonids (Cronin et al., 1993; Hall and Nawrocki, 1995; O'Connell et al., 1995; Hansen and Loeschcke, 1996). Mitochondrial DNA is maternally inherited and has a higher evolutionary rate relative to protein coding loci (Brown, 1983) and consequently has become a useful stock discrimination tool.

Random amplified polymorphic DNA (RAPD) uses PCR to amplify fragments of DNA with primers with random nucleotide sequences (Welsh and McClelland, 1990; Williams et al., 1990). Most fisheries applications of RAPD's have been at the species level (Dinesh et al., 1993; Bardakci and Skibinksi, 1994; Takagi and Taniguichi, 1995), although Macaranas et al. (1995) used RAPD's to distinguish populations of the freshwater red claw crayfish, *Cherax quadricarinatus*, in northern Australia, and a population specific RAPD marker was found in the marine shrimp *Penaeus vannamei* (Garcia et al., 1996).

In this paper we used three methods (allozymes, mtDNA, and RAPD's) to determine the genetic relations among orange roughy collected from four spawning sites off the east and south coasts of New Zealand.

Materials and methods

Tissue samples were collected on the RV *Tangaroa* from four spawning sites off the east and south coasts of New Zealand (Fig. 1). These sites were chosen because they are isolated by distances beyond the likely limit of larval drift (Zeldis et al., 1994). Each site supports significant fisheries, although the Waitaki fishery is relatively small and has declined quickly since development in the early 1990's (Annala and Sullivan[2]). Heart, liver, and muscle tissues were dis-

[2] Annala, J. H., and K. J. Sullivan. 1996. Report from the fishery assessment plenary, April–May 1996: stock assessments and yield estimates. Unpubl. Rep., Ministry of Fisheries, Greta Point Library, Wellington, New Zealand.

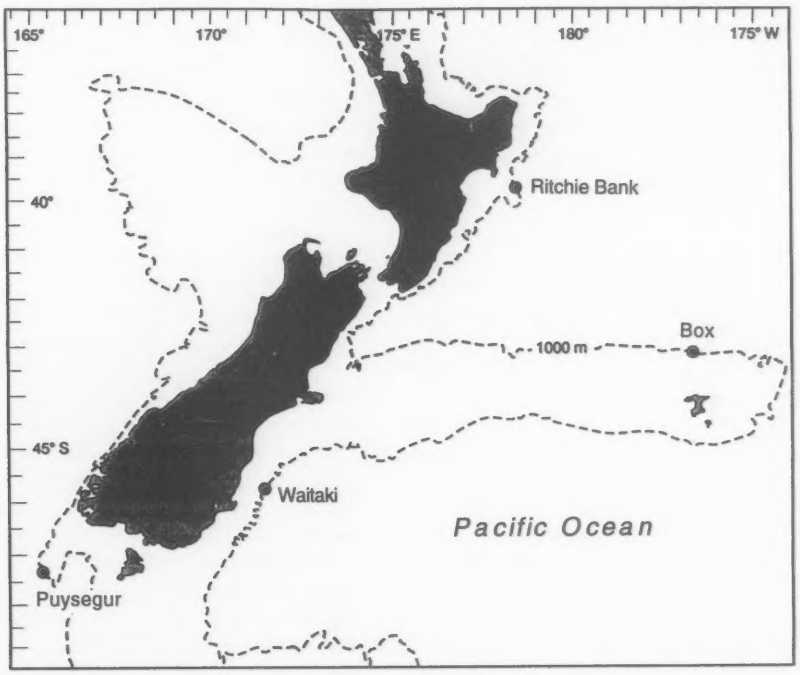

Figure 1

Location of orange roughy spawning sites around New Zealand sampled for genetic analyses. The dotted line represents the 1,000-m isobath.

sected from 100 specimens at three sites and from 50 specimens at Waitaki (Fig. 1). Tissue samples were frozen in liquid nitrogen at sea and stored at –70°C in the laboratory.

Allozyme electrophoresis

Eight enzyme systems were tested in heart, liver, and muscle tissues of orange roughy with cellulose acetate and starch gel electrophoresis following the methods in Smith (1986), except that BDH (British Drug House Chemicals Ltd, Poole, England) starch was substituted for Electrostarch (Electrostarch Company, USA).

DNA extraction

DNA was extracted from liver tissue of 50 orange roughy from each site. For each sample, 0.5 g of tissue was homogenized with 750 µL 4M guanidinium isothiocyanate in 8M urea and 2% sodium dodecyl sulfate (SDS) (Turner et al., 1989). DNA was extracted by mixing with an equal volume of phenol chloroform and centrifugation at 13,000 rpm for 5 min. The phenol-chloroform extraction was repeated and the aqueous fraction mixed with an equal volume of chloroform-isoamyl alcohol (24:1). Following centrifugation at 13,000 rpm, the aqueous fraction was mixed with two volumes of ethanol and the DNA allowed to precipitate at –20°C overnight. The DNA pellet was washed in 70% ethanol, air dried, and resuspended in 40 µL of sterile deionised water.

mtDNA amplification and restriction enzyme digestion

Three primer pairs were used to amplify the mtDNA. Amplification reactions were performed in 50-µL volumes in a Perkin Elmer Cetus DNA thermocycler: protocols followed those of Palumbi et al. (1991) and Cronin et al. (1993).The nucleotide sequences of the primers were the following:

D-loop	5'-ATAGTGGGGTATCTAATCCCA-3'
	5'-RCRCCCAAAGCTRRRRTTCTA-3'
	(Palumbi et al., 1991);
cytochrome *b*	5'-CCCTCAGAATGATA-TTTGTCCTCA-3'
	5'-TGACCTGAARAACCA-YCGTTG-3'
	(Palumbi et al.,1991); and
ND 5/6	5'-AATAGTTTATCCA-GTTGGTCTTAG-3'
	5'-TTACAACGATGGTTTTTCA-TAGTCA-3' (Cronin et al., 1993)

Twelve restriction endonucleases recognizing 4-base sites (*Bfa* I, *BstU* I, *Cfo* I, *Hae* III, *Hpa* II, *Mse* I, *Msp* I, *Nla* III, *Rsa* I, *Sal* I, *Sau* 3A, and *Taq* I) were used to digest the D-loop primer amplification products. Eleven restriction endonucleases recognizing 4-base sites (*Alu* I, *Bfa* I, *Cfo* I, *Hpa* II, *Msp* I, *Nar* I, *Rsa* I, *Sal* I, *Sau* 3A, *Taq* I, and *Tru* I) were used to digest the cytochrome *b* primer amplification products. The ND 5/6 primers produced between 1 and 3 amplification products in different specimens, therefore no restriction digests were undertaken with the PCR products.

For each primer pair and restriction enzyme, 24 fish were tested, 6 from each area. The restriction enzymes that showed polymorphisms were used to test 50 fish from each site. The amplified and digested DNA products were separated in 1.4% agarose gels and detected with ethidium bromide under a UV light (312 nm).

RAPD amplification and separation

Six individuals from each sample site were amplified with 24 RAPD primers. Each sample was amplified separately with a 10-base oligonucleotide primer from Operon (OperonTechnologies, Alameda, CA). These primers were randomly selected from Operon series A, D, E, and H primers, but all have a G+C content of 60–70%. Amplification reactions were performed in 50-µL volumes in a Perkin Elmer Cetus DNA thermocycler. Serial dilutions of DNA samples were tested initially to determine optimum DNA concentration for amplification (Fig. 2). The DNA concentration in each sample was estimated fluorometrically and appropriate volumes were used for amplification. Each reaction contained approximately 50 ng DNA in 10 mM Tris HCl (pH8.3), 30 ng single 10-base primer, 50 mM KCl, 2 mM $MgCl_2$, 100 mM each of *d*ATP, *d*CTP, *d*GTP, and *d*TTP, and 1 unit Taq DNA polymerase in Perkin Elmer PCR buffer. The reaction was overlaid with mineral oil and amplified. The thermocycler was programmed for 40 cycles of 1-min duration at 94°C, 1 min at 36°C, and 2 min at 72°C. Amplification products were separated in 1.4% agarose gels and detected with ethidium bromide staining under a UV light (312 nm). A DNA size-ladder was included in each gel. Control samples were amplified without a DNA template. Those primers that yielded variable fragment patterns were retested in the same fish. Primers producing repeatable fragment patterns in the initial six fish from each site were tested in 50 fish from each site. Polymorphisms were scored by the presence or absence of an amplification product at specific positions in the gel.

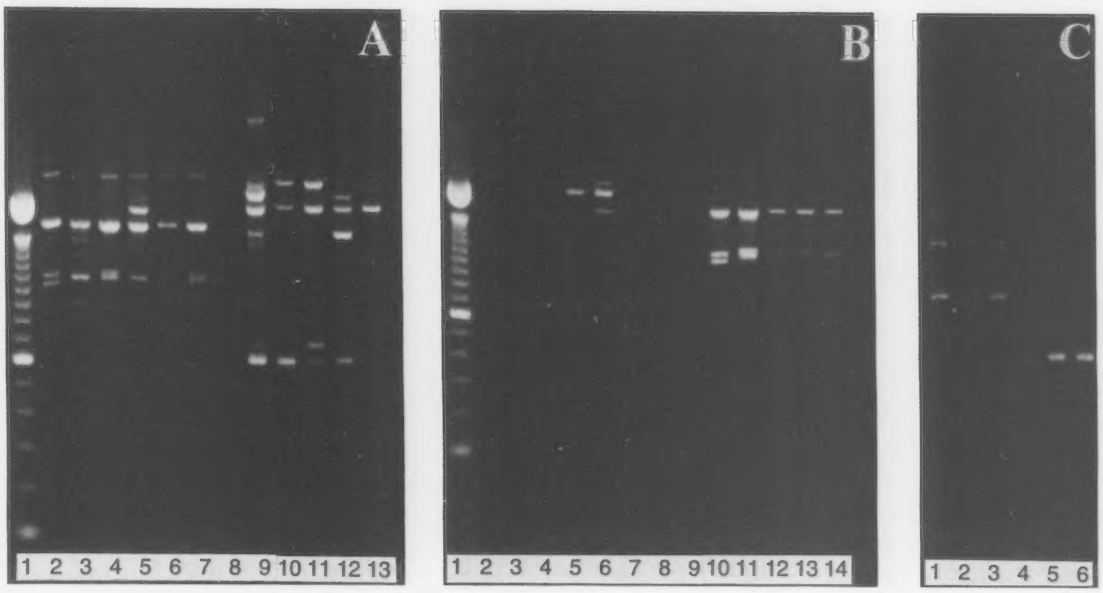

Figure 2

(**A**) Random amplified polymorphic DNA (RAPD) profiles in orange roughy generated with the primers A16 and E19. Lane 1 contains a DNA size-ladder (2,072–100 bp), lanes 2–7 represent orange roughy amplifed with primer A16, lane 8 contains no DNA template, and lanes 9–13 represent orange roughy amplifed with primer E19. Each amplified sample of orange roughy contained approximately 50 ng of DNA. (**B**) RAPD profiles in orange roughy generated with the primers A16 and E19 at different concentrations of DNA template. Lane 1 contains a DNA size-ladder (2,072–100 bp), lane 2 no DNA, lanes 3 and 4 contain 12.5 ng DNA amplified with E19, lanes 5 and 6 contain 50 ng DNA amplified with E19, and lanes 7 and 8 contain 200 ng DNA amplified with E19, lane 9 no DNA, lanes 10 and 11 contain 50 ng DNA amplified with A16, and lanes 12–14 contain 200 ng DNA amplified with A16. (**C**) RAPD profiles in orange roughy generated with the primer A14, lanes 1–3 contain 50 ng DNA, and lanes 4–6 represent the same samples at a concentration of 200 ng DNA.

Statistical analyses

Allozyme genotypes Genotypic frequencies were tested for Hardy-Weinberg equilibrium; weakly polymorphic loci (frequency of most common allele >0.95) were excluded. Rare heterozygotes were pooled with their nearest electrophoretic neighbor to reduce the number of cells with less than five observations. Allele frequencies were tested for heterogeneity among populations with contingency χ^2 tests with the BIOSYS software program (Swofford and Selander, 1981). To test for geographic structure, contingency χ^2 tests were undertaken on all pairwise combinations of populations. Probability levels were modified by the Bonferroni procedure for multiple tests according to Rice (1989).

The proportion of allozyme variation due to differentiation among populations was estimated with Nei's gene-diversity statistic G_{ST} (Nei, 1973), which is a multiallele estimator of Wright's F_{ST} statistics (Wright, 1951). Gene diversity is equal to

$$(H_T - H_S)/H_T,$$

where H_T = the total genetic diversity of all populations; and

H_S = the mean genetic diversity per population, calculated from the average expected heterozygosities.

Sampling error will produce differences in allele frequencies, even when samples are drawn from the same population, therefore a randomization test was used to test for differences due to sampling error (Elliott and Ward, 1992). One thousand randomizations were used, and the probability was estimated from the number of randomizations that were equal to or greater than the observed G_{ST}.

Gene diversity, G_{ST}, allows an estimation to be made of the number of migrants exchanged between populations per generation from the relation

$$N_e m = (1/G_{ST} - 1)/4,$$

where N_e = the effective population size; and
m = the rate of gene flow per generation.

It is assumed that m<<1 and that population differentiation is due to genetic drift and migration with no selection. Gene diversity was corrected to a "true" estimate by subtracting the G_{STnull} due to sampling error, derived from a randomization test (Elliott and Ward, 1992).

mtDNA Heterogeneity in haplotype frequencies in the total data was tested by the χ^2 randomization test described by Roff and Bentzen (1989) with the REAP package (McElroy et al., 1992). This method overcomes the problem of a large number of observed haplotypes at low frequency, by comparing χ^2 values in 1,000 random rearrangements of the data. In addition the χ^2 randomization test was applied to pairwise comparisons of all populations to test for geographic structure. Probabilities were estimated from the number of randomizations that were equal to or greater than the observed χ^2 value. The proportion of haplotype variation due to differentiation between populations was estimated by G_{ST} from the haplotype frequencies, as for allozymes. The number of migrants exchanged per generation was estimated from the relation

$$N_e m_f = (1/G_{ST} - 1)/2,$$

where m_f = female migration, modified to account for the maternal inheritance of mtDNA.

RAPD Standard genetic calculations are not immediately applicable to RAPD data because the fragments are dominant: individuals carrying two copies of an allele cannot be distinguished from individuals carrying one copy of the allele. Black (1995) has provided a set of programs for analyzing RAPD population data but points out that a number of assumptions have to be made. First, the observed fragments are dominant alleles and the absent fragments are recessive alleles. Second, the genotypes are in Hardy-Weinberg equilibrium and each observed polymorphism is biallelic: all the absent observations are produced by the same recessive allele and all the present observations are produced by a single dominant allele with or without the recessive allele. Each primer was scored for the presence or absence of fragments in the gel. Each fragment, regardless of primer, was treated as an independent locus. In most RAPD studies, fragments have been found that vary in staining intensity; we scored only fragments that were intensely stained, following Black (1993).

Random amplified polymorphic DNA allele frequencies were calculated from the presence or absence observations with the RAPDBIOS software program (Black, 1995) and then used in the BIOSYS software program (Swofford and Selander, 1981) for calculation of heterogeneity in allele frequencies as for allozyme data. The gene-diversity statistic G_{ST} ($=F_{ST}$) was calculated with the RAPDFST software program (Black, 1995); probabilities were calculated according to Workman and Niswander (1970). An estimation of the number of migrants exchanged per generation, $N_e m$, was estimated as for the allozyme data.

Results

Allozymes

Eleven enzyme loci were resolved in the four populations and allele frequencies are given in Appendix Table 1. Eight loci were sufficiently polymorphic (P<0.95) for Hardy-Weinberg tests. One out of a possible 32 tests (8 loci × 4 populations) showed a significant departure from Hardy-Weinberg equilibrium when a Bonferroni modified probability level was applied (*Idh-1** Puysegur, χ^2=13.99, 1 df, P<0.001).

The polymorphic loci were tested with a contingency χ^2 test. There was a significant heterogeneity among all four populations at 5 loci, *Est-1**, *Gpi-2**, *Idh-1**, *Idh-2**, and *Ldh-1**, with a Bonferroni-modi-

Table 1

Results of comparisons of allele frequencies at eleven loci and mtDNA haplotypes in four populations of orange roughy. df = degrees of freedom; P = probability value; and G_{ST} = gene diversity . * = significant at the 5% level with a Bonferroni-modified P for multiple tests.

Locus	χ^2	df	P	G_{ST}	P
*Cck-1**	7.93	6	0.243	0.006	0.277
*Est-1**	63.09	12	<0.001*	0.030	<0.001*
*Gpi-1**	4.70	9	0.860	0.002	0.889
*Gpi-2**	25.09	6	<0.001*	0.021	0.002*
*Idh-1**	26.91	9	0.001*	0.026	<0.001*
*Idh-2**	46.08	9	<0.001*	0.065	<0.001*
*Ldh-1**	19.02	3	0.003*	0.025	0.004*
*Ldh-2**	12.09	6	0.061	0.008	0.153
*Mdh-1**	11.20	6	0.082	0.012	0.066
*Mpi-1**	7.56	9	0.581	0.003	0.653
*Pgm-1**	2.58	6	0.860	0.001	0.839
all loci	226.2	81	<0.001	0.020	<0.001
mtDNA haplotypes	45.51		0.001	0.057	0.001

Table 2

Heterogeneity χ^2 pairwise comparisons for allozyme loci, mtDNA haplotypes, and random amplified polymorphic DNA (RAPD) fragments, among four populations of orange roughy. For the allozyme and RAPD data only those loci and fragments that were significant applying a Bonferroni-modified probability level are given.

Pair	Allozyme loci and probabilities	mtDNA haplotype probablities	RAPD primer fragments and probabilities
Ritchie and Box	NS NS	NS	
Ritchie and Waitaki	*Est-1** $P<0.001$	0.001	E19-3 $P<0.001$
Ritchie and Puysegur	*Gpi-2** $P<0.001$, *Idh-2** $P<0.001$	NS	A16-1 $P<0.001$
Box and Waitaki	*Est-1** $P<0.001$, *Idh-1** $P=0.001$ *Idh-2** $P<0.001$	NS	E19-3 $P<0.001$
Box and Puysegur	*Idh-2** $P<0.001$	NS	A16-1 $P<0.001$
Waitaki and Puysegur	*Est-1** $P<0.001$	0.003	E19-3 $P<0.001$

fied P for 11 loci (Table 1). To test for geographic structure, additional χ^2 tests were carried out on all pairwise combinations of populations. There was a significant heterogeneity for at least one locus between all population pairs, except Ritchie Bank and Box (Table 2).

The heterogeneity in the total data was confirmed by the gene diversity analysis (Table 1). When a Bonferroni-modified P is applied, the 5 loci show a G_{ST} significantly greater than that due to sampling error. Over all eleven loci G_{ST} was 0.020 (Table 1), indicating that around 2% of the observed genetic variation was due to differences among populations. From this estimate of G_{ST}, and by subtracting the G_{STnull}, the minimum number of effective migrants per generation (N_em) was 13.2 (Table 3). Individual pairs *of* N_em varied from 15.7 (Box and Waitaki) to 124 (Ritchie and Box).

Table 3

The estimated number of migrants exchanged per generation (N_em) for allozyme, mtDNA, and random amplified polymorphic DNA (RAPD) data sets of orange roughy.

Population	Allozyme	mtDNA	RAPD
Ritchie and Box	124.0	277.8	75.0
Ritchie and Waitaki	14.7	7.2	7.7
Ritchie and Puysegur	19.4	35.7	18.0
Box and Waitaki	15.7	18.3	7.8
Box and Puysegur	25.3	36.5	16.0
Waitaki and Puysegur	75.5	9.6	6.5
Total	13.2	9.8	7.0

mtDNA

The estimated size of the PCR amplified D-loop was 1,500 base pairs and that of the cytochrome *b* was 500 bp. Four restriction enzymes, *BstU* I, *Cfo* I, *Msp* I, and *Nla* III, produced two or more fragment patterns with the D-loop primers (e.g. Fig. 3) and were tested in all fish. For each area, a few fish samples failed to produce an amplification product; the same fish samples also failed to produce an amplification product with the RAPD primers. Four restriction enzymes, *Alu* I, *Bfa* I, *Rsa* I, and *Taq* I, showed variation in the first 24 fish tested with the cytochrome *b* primers, but the variation was limited to a single individual with each restriction enzyme. No further amplifications were undertaken with this set of primers. The numbers of haplotypes observed at each site are shown in Appendix Table 2. There is a significant heterogeneity in the total data (P=0.001), with only 1 out of 1,000 randomizations exceeding the original χ^2 value (Table 1). In pairwise comparisons of the four spawning populations (Table 2), significant differences were found between Ritchie Bank and Waitaki ($P<0.001$) and between Waitaki and Puysegur (P=0.001), but not in the other pairwise comparisons.

Gene diversity was estimated to be 0.057 (Table 1), which is significantly greater than that due to sampling error, and indicates that around 6% of the observed genetic variation is due to differences among populations. From this estimate of G_{ST}, and by subtracting the G_{STnull}, the minimum number of female migrants per generation (N_em_f) among the four populations was estimated to be 9.8 (Table 3). The pairwise values varied from 7.2 (Ritchie and Waitaki) to 277.8 (Ritchie and Box).

RAPD

Seven primers tested in 24 orange roughy produced clear DNA fragments and the same profiles in repeat tests. The primers (and their sequences 5' to 3')

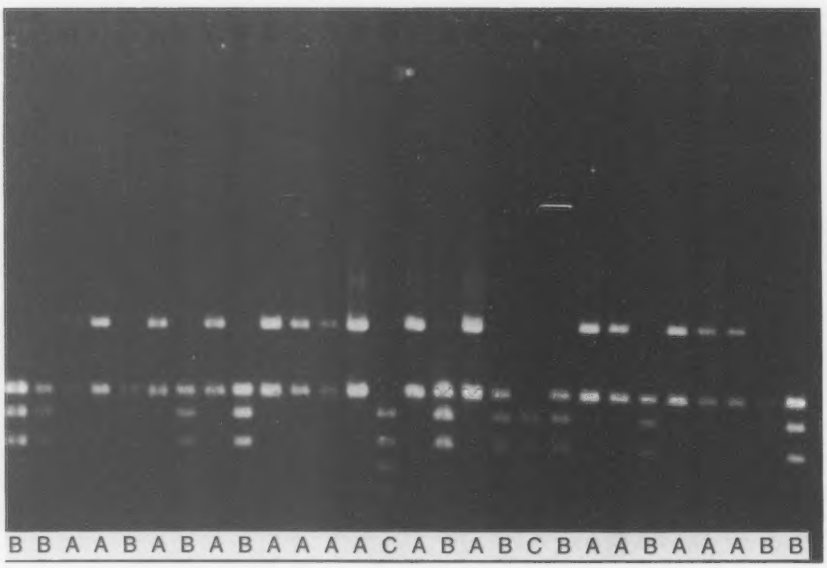

Figure 3

Photograph of *Cfo 1* haplotypes in the D-loop region of mtDNA amplified from 28 orange roughy. Haplotype A = 2 fragments, B = 3 fragments, and C = 4 fragments.

were A14 (TCTGTGCTGG), A15 (TTCCGAACCC), A16 (AGCCAGCGAA), A17 (GACCGCTTGT), D15 (CATCCGTGCT), E19 (ACGGCGTATG), and H17 (CACTCTCCTC). The number of scored fragments varied from 1 to 6 per primer, and the size of the fragments from 0.6 to 2.8 kb. Fragments that could be scored were numbered in decreasing order of electrophoretic mobility (e.g. primer A14 fragment 1 = A14-1); each individual fish was scored for the presence or absence of each fragment. Repeat tests on some individuals did not produce repeatable patterns for some weakly staining fragments, therefore presence or absence of each fragment was not scored for these fragments. Omitting the DNA template from the PCR reaction (i.e. negative control) failed to produce fragments. The amount of DNA in the initial extractions varied tenfold between samples. Excess DNA, 250 ng, produced different fragment patterns with some primers (Fig. 2), therefore all amplifications were optimized to contain a 50-ng template of DNA.

The estimated allele frequencies are given in Appendix Table 3. Two out of 29 primer fragments (A16-1, E19-3) revealed a significant heterogeneity among populations when a heterogeneity χ^2 test with a modified probability for multiple tests was applied (Table 4). Pairwise comparisons showed significant differences between all pairs of populations except Ritchie Bank and Box at these two primer fragments (Table 2). The heterogeneity in the total data set was confirmed by the G_{ST} tests (Table 4). The effective number of migrants per generation was estimated to be 7.0 from the overall G_{ST}, minus G_{STnull} due to sampling error (Table 3), as described for allozymes. Pairwise values varied from 6.5 (Waitaki and Puysegur) to 75 (Ritchie and Box).

Discussion

There was significant heterogeneity in the allozyme data set at five loci (Table 1) which indicated that the population samples had not been taken from a single panmictic stock. Pairwise comparisons showed that there were significant differences between all pairs of spawning populations except the two northern populations at Ritchie Bank and Box (Fig. 1). The RAPD data also showed a significant heterogeneity that indicated that the population samples had been taken from more than one genetic unit stock. There were no area-specific RAPD fragments in orange roughy, as have been reported in marine prawns (Garcia et al., 1996) and freshwater crayfish (Macaranas et al., 1995), but there were differences in

frequencies of two primer fragments (A16-1, E19-3, Table 4). As with the allozyme data, there were differences between all pairwise comparisons, with the exception of those samples taken at Ritchie Bank and Box (Table 2).

The mtDNA data also showed a significant heterogeneity in the total data set but demonstrated less genetic differentiation than the allozyme and RAPD data sets, with only two pairwise comparisons showing a significant difference (Table 2). However all three methods, which have measured different parts of the genome, gave similar results of low genetic exchange among the four populations (Table 3). None of the estimates of N_em are true estimates because our data sets are biased in favor of polymorphic markers, which will tend to inflate the G_{ST} estimate; such estimates of N_em (Table 2) can be used to compare only relative levels of geneflow between areas (Ferguson, 1994). In this respect there is 8–10 times as much gene flow between Ritchie Bank and Box than between these sites and Waitaki, when measured with allozymes and RAPD's, and 15–38 times as much with mtDNA (Table 3). Significant genetic differences between spawning groups provides evidence of genetic isolation, and thus the data reveal three genetic groups: 1) Puysegur, 2) Waitaki, and 3) Ritchie Bank and Box (Table 2).

There are problems with RAPD analyses that may preclude them from use as stock markers for orange roughy. Because RAPD markers are dominant, a number of assumptions have to be made to analyze the data (Lynch and Milligan, 1994). Some of these assumptions, in particular that fragments with the same electrophoretic mobility are genetically identical and that absent fragments represent the same DNA fragment, may not be valid. Fragments that exhibited weak staining activity were not scored, so that there is a subjective element when scoring RAPD gels.

In the absence of breeding studies, the allelic nature of presence or absence of RAPD fragments may be suspect. Garcia and Benzie (1995) reported an extra RAPD fragment in prawn larvae that was absent in adults, although they found Mendelian inheritance of other RAPD markers. Unlike the other two genetic methods, there are no internal checks that can be used to fit RAPD phenotypes to a genetic model: with allozymes there is an expected gel phenotype for each enzyme and all alleles are equally expressed; with mtDNA the size of the restricted fragments should add up to the size of the undigested fragment.

Some primers produced weak fragments that were not repeatable in reamplifications. These weak fragments may be produced by excessive PCR cycles; Bell and DeMarini (1991) have shown that by increasing the number of PCR cycles above 30, nonspecific DNA products can be obtained. However, in our preliminary amplifications in extracting DNA from frozen tissue samples, less than 40 cycles produced faint fragment patterns for most primers; thus 40 cycles were used as a standard. The RAPD technique has been shown to be very sensitive to changes in concentration of primer, concentration of template, annealing temperature, and the concentration of magnesium ions, all of which can affect the number and intensity of bands (Devos and Gale, 1992; Ellsworth et al., 1993; Patwary et al., 1993; Penner et al., 1993). We sought to avoid these problems by standardizing DNA quantities prior to amplification, performing all amplifications on the same thermocycler, and using the same batch of chemicals. Tissue samples from the four spawning sites were collected and stored under similar conditions.

Table 4

Heterogeneity χ^2 tests and gene diversity (G_{ST}) for seven random amplified polymorphic DNA (RAPD) primers in four populations of orange roughy. df = degrees of freedom; P = probability value; G_{ST} = gene diversity. (* = significant at Bonferroni-modified P for multiple tests).

Primer and fragment	χ^2 (3 df)	P	G_{ST} (3 df)	P
A14-1	2.820	0.422	0.010	0.415
A14-2	3.306	0.347	0.012	0.341
A14-3	9.089	0.028	0.032	0.031
A15-1	1.543	0.672	0.006	0.671
A15-2	8.189	0.042	0.029	0.044
A15-3	3.593	0.309	0.013	0.299
A15-4	2.138	0.544	0.008	0.540
A16-1	16.921	<0.001*	0.079	<0.001*
A16-2	1.473	0.688	0.005	0.685
A16-3	6.874	0.076	0.024	0.087
A16-4	5.072	0.167	0.019	0.156
A16-5	0.513	0.916	0.002	0.915
A17-1	2.138	0.544	0.008	0.540
A17-3	6.715	0.082	0.025	0.073
D15-1	5.436	0.143	0.018	0.178
D15-2	2.114	0.549	0.008	0.513
D15-3	3.862	0.277	0.014	0.280
D15-4	1.678	0.642	0.007	0.615
E19-1	8.080	0.044	0.300	0.043
E19-2	9.283	0.026	0.032	0.033
E19-3	23.079	<0.001*	0.082	<0.001*
E19-4	6.558	0.087	0.026	0.071
E19-5	2.680	0.444	0.010	0.423
E19-6	0.823	0.844	0.002	0.887
H17-1	3.824	0.281	0.014	0.268
H17-2	3.119	0.374	0.012	0.343
H17-3	0.776	0.855	0.003	0.863
H17-4	2.155	0.541	0.007	0.604
H17-5	0.500	0.919	0.002	0.913
Total (87 df)	164.66	<0.001	0.019	<0.001

Given the technical problems with RAPD's, we would recommend them only when other genetic methods have failed to reveal polymorphisms. Techniques such as PCR-RFLP of mtDNA, or allozymes, yielded fewer polymorphisms per unit of laboratory time than did RAPD's but still produced sufficient polymorphisms to detect population structure in orange roughy. Our allozyme data set indicated a higher level of genetic subdivision than that found with mtDNA in orange roughy. This result is surprising in view of the relatively higher rate of evolution of mtDNA (Brown, 1983), and it is possible that other regions of the mitochondrial genome, or use of additional restriction enzymes, might reveal more genetic variation. Several studies of marine organisms have detected greater genetic subdivision with mtDNA than with allozyme markers (e.g. Reeb and Avise, 1990), although there are examples of the reverse in the fisheries literature (Grewe et al., 1994; Ward et al., 1994). It is possible that the allozyme markers are under selection (Koehn et al., 1980) and are responding to short-term population events rather than to historical events due to reproductive isolation.

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Appendix

Appendix Table 1

Allele frequencies for 11 allozyme loci tested in four populations of orange roughy.

Locus	Allele (*n*=no. of fish)	Ritchie	Box	Waitaki	Puysegur
*Cck-1**	1	0.494	0.500	0.596	0.551
	2	0.489	0.500	0.404	0.444
	3	0.017	0.000	0.000	0.005
	n	90	81	47	99
*Est-1**	1	0.051	0.160	0.093	0.152
	2	0.222	0.229	0.372	0.250
	3	0.709	0.606	0.430	0.585
	4	0.006	0.005	0.006	0.013
	5	0.013	0.000	0.000	0.000
	n	79	94	43	99
*Gpi-1**	1	0.515	0.551	0.553	0.517
	2	0.232	0.253	0.245	0.265
	3	0.253	0.191	0.191	0.214
	4	0.000	0.006	0.001	0.004
	n	99	89	47	99
*Gpi-2**	1	0.015	0.033	0.042	0.058
	2	0.970	0.944	0.948	0.860
	3	0.015	0.022	0.010	0.081
	n	99	90	48	99
*Idh-1**	1	0.030	0.011	0.106	0.083
	2	0.970	0.979	0.883	0.897
	3	0.000	0.005	0.011	0.021
	4	0.000	0.005	0.000	0.000
	n	99	94	47	99
*Idh-2**	1	0.417	0.442	0.180	0.196
	2	0.583	0.548	0.809	0.793
	3	0.000	0.005	0.011	0.011
	4	0.000	0.005	0.000	0.000
	n	96	94	47	94
*Ldh-1**	1	1.000	0.983	0.979	0.931
	2	0.000	0.017	0.021	0.069
	n	96	90	47	99
*Ldh-2**	1	0.000	0.000	0.011	0.000
	2	1.000	0.980	0.989	0.980
	3	0.000	0.020	0.000	0.020
	n	96	99	47	99
*Mdh-1**	1	0.625	0.729	0.656	0.745
	2	0.375	0.271	0.344	0.250
	3	0.000	0.000	0.000	0.005
	n	96	94	48	98
*Mpi-1**	1	0.037	0.027	0.052	0.057
	2	0.957	0.968	0.948	0.943
	3	0.000	0.005	0.000	0.000
	4	0.005	0.000	0.000	0.000
	n	94	94	48	97
*Pgm-1**	1	0.116	0.144	0.117	0.126
	2	0.879	0.850	0.883	0.874
	3	0.005	0.006	0.000	0.000
	n	99	90	47	99

Appendix Table 2

Numbers of composite mtDNA D-loop haplotypes observed in four populations of orange roughy. The composite haplotypes are based on the restriction enzymes *BstU* I, *Cfo* I, *Msp* I, and *Nla* III.

Haplotype	Ritchie	Box	Waitaki	Puysegur
AABA	21	19	5	14
BBBA	11	18	21	7
ACBA	0	0	2	0
AAAA	2	0	0	0
AABB	1	1	1	3
AABC	1	0	0	0
AACA	1	0	0	0
ABBA	4	4	6	10
BABA	2	6	6	6

Appendix Table 3

Random amplified polymorphic DNA (RAPD) fragment frequencies, calculated by assuming a biallelic system in Hardy-Weinberg equilibrium, in four populations of orange roughy.

Locus	Allele (*n*=no. of fish)	Ritchie	Box	Waitaki	Puysegur	Locus	Allele (*n*=no. of fish)	Ritchie	Box	Waitaki	Puysegur
A14-1	1	0.00	0.021	0.00	0.021	D15-2	1	0.426	0.542	0.500	0.489
	2	1.00	0.979	1.00	0.979		2	0.574	0.458	0.500	0.500
	n	44	48	42	40		*n*	44	48	42	40
A14-2	1	0.454	0.417	0.417	0.330	D15-3	1	0.629	0.708	0.583	0.745
	2	0.546	0.583	0.583	0.670		2	0.361	0.292	0.417	0.255
	n	44	48	42	40		*n*	44	48	42	40
A14-3	1	0.306	0.188	0.167	0.394	D15-4	1	0.083	0.063	0.042	0.043
	2	0.694	0.813	0.833	0.596		2	0.907	0.938	0.958	0.957
	n	44	48	42	40		*n*	44	48	42	40
A15-1	1	0.009	0.00	0.00	0.00	E19-1	1	0.269	0.292	0.142	0.330
	2	0.991	1.00	1.00	1.00		2	0.731	0.708	0.858	0.670
	n	44	48	42	40		*n*	43	48	42	38
A15-2	1	0.806	0.792	0.708	0.638	E19-2	1	0.148	0.271	0.042	0.149
	2	0.194	0.208	0.292	0.362		2	0.852	0.729	0.958	0.851
	n	44	48	42	40		*n*	43	48	42	38
A15-3	1	0.028	0.042	0.042	0.00	E19-3	1	0.639	0.646	0.125	0.521
	2	0.972	0.958	0.958	1.00		2	0.361	0.354	0.875	0.479
	n	44	48	42	40		*n*	43	48	42	38
A15-4	1	0.009	0.021	0.00	0.00	E19-4	1	0.093	0.021	0.083	0.021
	2	0.991	0.979	1.00	1.00		2	0.898	0.979	0.917	0.979
	n	44	48	42	40		*n*	43	48	42	38
A16-1	1	0.49	0.46	0.33	0.74	E19-5	1	0.056	0.042	0.00	0.021
	2	0.51	0.54	0.67	0.26		2	0.944	0.958	1.00	0.979
	n	43	48	42	38		*n*	43	48	42	38
A16-2	1	0.019	0.00	0.00	0.021	E19-6	1	0.769	0.708	0.708	0.745
	2	0.981	1.00	1.00	0.979		2	0.231	0.292	0.292	0.255
	n	43	48	42	38		*n*	43	48	42	38
A16-3	1	0.278	0.271	0.125	0.149	H17-1	1	0.046	0.00	0.00	0.021
	2	0.722	0.729	0.875	0.851		2	0.954	1.00	1.00	0.979
	n	43	48	42	38		*n*	44	48	42	38
A16-4	1	0.694	0.708	0.583	0.564	H17-2	1	0.806	0.708	0.708	0.713
	2	0.306	0.292	0.417	0.436		2	0.194	0.292	0.292	0.287
	n	43	48	42	38		*n*	44	48	42	38
A16-5	1	0.019	0.021	0.00	0.021	H17-3	1	0.769	0.792	0.708	0.745
	2	0.981	0.979	1.00	0.979		2	0.231	0.208	0.292	0.255
	n	43	48	42	38		*n*	44	48	42	38
A17-1	1	0.009	0.021	0.00	0.00	H17-4	1	0.731	0.708	0.708	0.638
	2	0.991	0.979	1.00	1.00		2	0.269	0.292	0.292	0.362
	n	43	48	42	38		*n*	44	48	42	38
A17-3	1	0.009	0.00	0.00	0.053	H17-5	1	0.019	0.021	0.042	0.021
	2	0.991	1.00	1.00	0.947		2	0.981	0.979	0.958	0.979
	n	43	48	42	38		*n*	44	48	42	38
D15-1	1	0.111	0.188	0.042	0.074						
	2	0.889	0.813	0.958	0.926						
	n	44	48	42	40						

Survival of chinook salmon, *Oncorhynchus tshawytscha*, from a spawning tributary of the Rakaia River, New Zealand, in relation to spring and summer mainstem flows

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Abstract.—To characterize the impact of spring floods on the survival of juvenile chinook salmon in the unstable, braided rivers on the east coast of New Zealand's South Island, I examined correlations between spring and summer flows in the mainstem of the Rakaia River and fry-to-adult survival for chinook salmon spawning in a headwater tributary. Flow parameters that were investigated included mean flow, maximum flow, and the ratio of mean to median flow (an index of flow variability), calculated during peak downriver migration of ocean-type juveniles (August to January). Survival was uncorrelated with mean or maximum flow but was positively correlated with the ratio of mean to median flow during spring (October and November). The correlation suggests that pulses of freshwater entering the ocean during floods may buffer the transition of fingerlings from fresh to saline waters and thus partly compensate for the lack of an estuary on the Rakaia River. A positive correlation between spring flow variability and the proportion of ocean-type chinook in relation to stream-type chinook is also consistent with this hypothesis. All correlations were relatively weak, reinforcing earlier results that production is primarily controlled by marine influences. These findings further demonstrate the considerable ability of chinook salmon to adapt to new habitats.

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To understand the population dynamics of anadromous Pacific salmonids (*Oncorhynchus* spp.), it is important to isolate and characterize the influence of varying environmental factors on annual production. In the course of their life cycle salmon inhabit a succession of freshwater and marine environments, where prospects for survival depend on prevailing conditions. Spawning and incubation success may be adversely affected by substrate disturbance during floods; the suitability of riverine waters as habitat for rearing juveniles is dependent on both flow and temperature and may be reduced by flows that are too low or too high; and adult survival within the marine environment is at least partly determined by environmentally controlled factors such as oceanic water masses and the availability of suitable prey. Numerous studies have demonstrated significant correlations between environmental variables and indices of survival and growth, at scales ranging from local to global. Although correlation analysis in fisheries studies has been criticized for its potential for misuse and for a propensity to produce weak results of little practical value (Walters and Collie, 1988), other authors have noted that provided the method is used with discretion, biologically meaningful results can be derived (Kope and Botsford, 1990).

Despite the importance of instream habitats for rearing juvenile chinook salmon (*O. tshawytscha*), the relation between flow and brood year survival has received comparatively little attention. Interannual trends in the abundance of chinook salmon in the Fraser River, British Columbia, have been linked to flow variations in the mainstem (Beamish et al., 1994) and in the Nechako River tributary (Bradford, 1994). In the former study, annual production was inversely related to mean annual discharge, whereas in the latter study, juvenile survival in the upper Nechako appeared to decline as a result of flow diversion for hydroelectric generation, and the proportion of spawning fish using the upper river appeared to be negatively correlated with August flows. However, in the Nechako River study, as in some other studies linking downriver migration to river flows (e.g. Kjelson et al., 1982), low flows were often associated with increased water temperatures, making it difficult to differentiate between flow-related and temperature-related effects. Williams and Matthews (1995) found that survival of Snake River spring and summer chinook salmon juveniles was reduced during low flow conditions but concluded that these

losses were primarily due to problems with passage through hydroelectric dams rather than to low discharge per se. The effects of flow variability on survival have also received little attention. Increased downstream movement of newly emerged salmonid fry following sudden increases in discharge has been well documented (e.g. Irvine, 1986; Saltveit et al., 1995), but only rarely has flow variability been used as a predictor variable in population studies (Berggren and Filardo, 1993).

Whenever brood year survival is estimated from stock-recruitment or similar data, a search for correlations between river flow and survival will usually involve deriving a single flow index, such as the annual mean, for each cohort. Most such studies conducted to date have used flow averaged over periods from three months (Kope and Botsford, 1990) to one year (Beamish et al., 1994), but it is by no means obvious that these are the most informative or biologically meaningful parameters to use. A single catastrophic flood during the incubation period may cause large-scale destruction of redds and loss of alevins through bed scour (Montgomery et al., 1996) without having much effect on the mean annual flow. Prior to smolting, fry may be susceptible to short-term floods that carry them prematurely into seawater, when the same floods a few months later would have little impact. In addition, mean flow is not necessarily the most relevant statistic for characterizing flow regimes; it is possible that in the two examples given above, some other parameter (such as maximum flow or the coefficient of variation) might be more informative (e.g. Hvidsten and Hansen, 1988). For example, in New Zealand, where high flow variability is a defining characteristic of riverine ecosystems (Biggs, 1995), statistics such as the proportion of the time the flow exceeds three times the median (Clausen and Biggs, in press) and the ratio of mean flow to median flow (Jowett, 1990), have been successful in elucidating relations between flow regime and biological parameters. To explore fully the relation between flow and survival, therefore, it is necessary to consider not only the type of flow statistic that is likely to be of interest but also the duration and seasonal timing of the period over which the statistic is to be calculated.

Since the introduction of fall-run Sacramento River stock to New Zealand in the early 1900's (McDowall, 1994a; Quinn et al., 1996), chinook salmon have maintained self-sustaining populations in all major rivers on the east coast of the South Island (McDowall, 1990; Quinn and Unwin, 1993). Like most New Zealand rivers, these rivers (whose wide, braided shingle beds drain steeply mountainous catchments on the South Island main divide) are characterized by highly variable flows (Jowett and Duncan, 1990), flooding quickly whenever snow and ice melt in the headwaters is augmented by heavy orographic rainfall. These floods occur at any time of year but are particularly common in spring. In rivers such as the Rakaia they cause massive bed movement (Ibbitt, 1979) and reduce the abundance and diversity of invertebrate fauna (Sagar, 1986) for up to one month afterwards. The impact of these events on seaward-migrating juvenile chinook has generated some debate. Several authors have remarked that survival of New Zealand chinook fry may be adversely affected during floods (McDowall, 1990; Flain[1]). Other studies suggest that, although some fry may be lost during extreme floods, flow fluctuations in a more typical season do not have a serious negative impact on migration (Hopkins and Unwin, 1987).

Chinook salmon spawning populations in Glenariffe Stream, a headwater spawning tributary of the Rakaia River (Fig. 1), have been monitored since 1965 by means of an upstream counting fence (Quinn and Unwin, 1993). In this study I analyzed brood year survival, for chinook spawning in Glenariffe Stream, in relation to Rakaia mainstem discharge during spring and summer (August to January). My primary objectives were to examine various flow statistics as possible correlates with survival and to determine the sensitivity of any resulting correlations to changes in the interval used to calculate each statistic. A secondary objective was to examine evidence that spring floods were detrimental to brood year survival.

Chinook salmon in New Zealand

New Zealand chinook salmon are broadly similar to their Sacramento ancestors in terms of both their general life history (Unwin, 1986) and genetic make up (Quinn et al., 1996). Present day stocks comprise a mixture of ocean- and stream-type fish (Gilbert, 1913; Healey, 1983), corresponding to juveniles that spend 3–6 mo or 12–15 mo in fresh water before entering the ocean (Unwin and Lucas, 1993). In the Rakaia River, the most thoroughly studied of the major salmon producing rivers, ocean-type fish make up about two-thirds of the returning adults (Quinn and Unwin, 1993).

The migration patterns of age-0+ juvenile chinook salmon in the Rakaia River and a key spawning tributary, Glenariffe Stream (Fig. 1), have been studied in some detail, and are relatively well understood (Unwin, 1986; Hopkins and Unwin, 1987). From

[1] Flain, M. 1982. Quinnat salmon runs, 1965–1978, in the Glenariffe Stream, Rakaia River, New Zealand. Occasional Publ 28, N.Z. Ministry of Agriculture and Fisheries, Fisheries Research Div., 22 p. [Copy held at NIWA, Christchurch, New Zealand.]

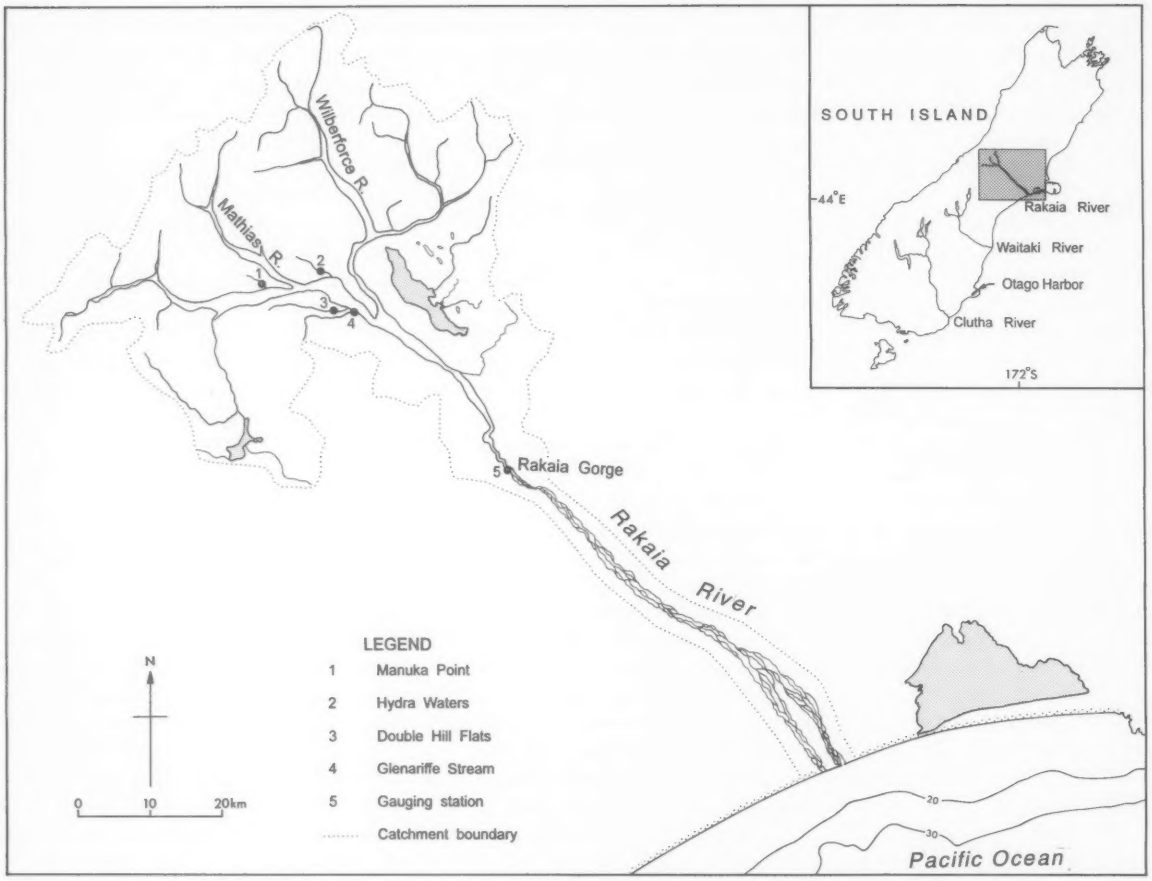

Figure 1

The South Island of New Zealand and the Rakaia River catchment, showing geographical features referred to in the text, the four main headwater tributaries used by spawning chinook salmon (1–4), and the 20-m and 30-m isobaths off the Rakaia mouth.

August to October (late winter to mid spring), large numbers of newly hatched fry emerge from the gravel in Glenariffe Stream and other spawning areas and begin to move downstream within 24 h of emergence. This migration appears to be driven by population pressure; the rearing capacity of Glenariffe Stream has been estimated at less than 100,000 fry, whereas annual fry production can exceed 3.7 million (Unwin, 1986). A second wave of larger fry, representing individuals remaining in their natal stream for up to 3 months, enters the upper river from November to January, but in Glenariffe Stream these fry represent less than 10% of the total production. This pattern appears to be typical for chinook populations within their native range (e.g. Lister and Walker, 1966; Reimers, 1973; Healey, 1991).

Within the upper reaches of the Rakaia River, fry quickly take up residence along the margins of the braided channels, where there is an abundance of suitable rearing habitat (Glova and Duncan, 1985). Aquatic invertebrates, predominantly *Deleatidium* spp., are the primary prey in spring, but in summer the diet of fry is dominated by terrestrial species and chironomids (Sagar and Glova, 1987). From mid-August fingerlings gradually disperse downriver, growing steadily as the season progresses and reaching the lower river in mid-October at about 60–80 mm fork length (FL) (Hopkins and Unwin, 1987). Fingerlings remain abundant in the lower river until early February but show little tendency to increase in size; thus there appears to be a steady emigration of 90-day fingerlings into marine waters with continual replacement from upriver (Hopkins and Unwin, 1987). Similar patterns of movement have been observed in other New Zealand stocks (Davis and Unwin, 1989), in their ancestral Sacramento River (Kjelson et al., 1982), and elsewhere in North America (Healey, 1991). Mean FL at seawater entry

for these fingerlings is consistent with the back-calculated mean FL at seawater entry for ocean-type adults of Rakaia origin (Unwin and Lucas, 1993), confirming the importance of springtime mainstem rearing for ocean-type fry. Freshwater residence patterns of juvenile stream-type fish are less well understood, but there is some evidence that an initial period of tributary rearing lasting 3–6 mo is followed by mainstem rearing for the remainder of the first year (Unwin, 1986).

In the absence of a commercial marine fishery for salmon, very little is known about the marine phase of the salmon life cycle. Adult chinook are piscivorous and appear to feed opportunistically within the pelagic zone, although prey diversity is low and food availability is potentially limited by annual fluctuations in prey abundance (James and Unwin, 1996). Brood year survival rates for both naturally and hatchery-produced chinook of Rakaia origin vary by up to two orders of magnitude and appear to be predominantly related to marine influences (Unwin, in press). However, these results do not preclude the possibility that survival may also be partly influenced by conditions within the freshwater environment.

Data sources and methods

The Rakaia River

The Rakaia River is a large, braided, glacier-fed river draining a 2,910 km^2 catchment that spans 70 km of the Southern Alps and rises to 2,800 m. Apart from a gentle 5-km gorge where the flow is briefly confined to a single channel, the river occupies an unstable, highly braided shingle bed up to 5 km wide (see Fig. 2 of Glova and Duncan, 1985). After collecting water from two major headwater tributaries (the Mathias and Wilberforce), the lower section (90 km) of the river flows directly into the Pacific Ocean with no significant tributary input. All major salmon spawning waters are located upstream of the Wilberforce confluence (Fig. 1). River gradient is virtually constant below this point, averaging 4.5 m/km, and the river discharges into the ocean via a small freshwater lagoon extending inland from the open sea for less than 100 m. The term "lagoon" is used in preference to "estuary" because there is no ebb and flow of the tide (although there is a tidal backup of fresh water) and because the area supports few, if any, predominantly estuarine life forms.[2] A detailed description of the river and its catchment is given by Bowden.[3]

Continuous flow data for the Rakaia River have been collected since 1959 by means of recorders at the downstream end of the gorge, 62 km above the mouth. For the purposes of this study, all flow statistics were calculated from the daily mean discharge (Q). Discharge (annual mean 200 m^3/s) shows a moderately seasonal pattern, monthly means varying from 127 m^3/s in July to 265 m^3/s in November.[3] The mean annual flood (the average of the annual maximum flow) is 1 448 m^3/s, with a peak instantaneous discharge of 5,600 m^3/s (estimated to have a return period of 60 yr) recorded in January 1994. The bankfull discharge (the instantaneous flow which results in complete inundation of the river bed as individual braids coalesce) ranges from 800 m^3/s just below the gorge to about 2,500 m^3/s in the lower river. Flood waters move rapidly downriver, typically reaching the mouth 8–12 h after passing through the gorge, although peak velocity increases with flood intensity, and travel times as short as 3.5 h over 40 km have been observed.[4,5] Over the months relevant to this study, daily mean water temperatures in the lower river (23 km above the mouth) range from 6°C in August to 16°C in January (Unwin, 1986).

Glenariffe Stream spawning runs

Glenariffe Stream is a spring-fed tributary joining the Rakaia River 100 km above its mouth at an altitude of 430 m (Fig. 1). The flow regime is exceptionally stable, with a mean discharge of 3.4 m^3/s and a maximum recorded discharge (over a seven-year period) of 16 m^3/s. Chinook salmon spawning runs in Glenariffe Stream have been monitored annually by means of a counting fence installed in 1965 (Quinn and Unwin, 1993; Flain[1]). The modal age-at-maturity is three years, with smaller numbers of 2-year and 4-year-olds and very few 5-year-old fish. The angler interception rate varies little between years, typically ranging from 30% to 40%.[6,7] Since 1980,

[2] Eldon, G. A., and A. J. Greager. 1983. Fishes of the Rakaia Lagoon. Fisheries Environmental Report 30. N. Z. Ministry of Agriculture and Fisheries, Fisheries Res. Div., Christchurch, 65 p. [Copy held by NIWA, Christchurch, New Zealand.]

[3] Bowden, M. J. 1983. The Rakaia River and catchment—a resource survey, vol. 2. North Canterbury Catchment Board and Regional Water Board, Christchurch, New Zealand, 101 p. [Copy held by NIWA, Christchurch, New Zealand.]

[4] 1997. Unpubl. data, NIWA, Christchurch, New Zealand.

[5] Horrel, G. 1997. Canterbury Regional Council, PO Box 345, Christchurch, New Zealand. Personal commun.

[6] Unwin, M. J., and S. F. Davis. 1983. Recreational fisheries of the Rakaia River. Fisheries Environmenal Report 30. New Zealand Ministry of Agriculture and Fisheries, Fisheries Research Division, Christchurch, New Zealand. [Copy held by NIWA, Christchurch, New Zealand.]

[7] Millichamp, R. 1997. North Canterbury Fish and Game Council, 3 Horatio Street, Christchurch, New Zealand. Personal commun.

spawning stocks have been supplemented by hatchery releases, but scale-pattern analysis and coded-wire tag recoveries of spawning fish intercepted at the fence allow each run to be partitioned into hatchery-reared and naturally spawning components (Unwin and Glova, 1997). The stability of the flow regime ensures that pre-emergence mortality of ova and alevins is not flow-dependent and is reflected by the lack of interannual variation in egg to fry survival for naturally spawning fish (Unwin, 1986; Unwin, in press). Over five years (1973–76, and 1992) of record egg-to-fry survival ranged from 38 to 52% and averaged 48%. On this basis, annual production can be consistently expressed in terms of the number of fry leaving Glenariffe Stream (Unwin, 1997).

For this study, I used the data set in Table 1 of Unwin (1997), summarizing fry-to-adult survival (S) for the 26 years from 1965 to 1990, expressed as live adult spawners reaching Glenariffe Stream (summed over all year classes for each cohort) per 10,000 fry. These data are reproduced here as Table 1. Survival ranged from 1.3 (for the 1971 brood year) to 117 (for the 1973 brood year), with an annual mean of 8 spawners per 10,000 fry (0.079%). These data were log-normally distributed (Unwin, 1997); therefore I used log-transformed values for all calculations (see also Bradford, 1995).

Data analysis

For each year from 1965 to 1990, I calculated mean flows ($\overline{Q}$) for each calendar month, for the two three-month periods August–October ("spring") and November–January ("summer"), and for the full six months. As indices of flow variability, I determined the maximum flow ($\hat{Q}$), and the ratio of the mean to the median flow ($\overline{Q}/\tilde{Q}$), for the same monthly, three-monthly and six-monthly intervals. Although other measures of flow variability are possible, such as skewness, coefficient of variation (CV), and baseflow index (which measures the ratio of the volume of base flow to the volume of total runoff), these all tend to be highly correlated and there is no one measure which represents the "best" index (Jowett and Duncan, 1990). I chose $\overline{Q}/\tilde{Q}$ because it is more robust (i.e. insensitive to extreme outliers) than statistics

Table 1

Spawning population size, fry production, adult returns, and fry-to-adult survival (adults per 10,000 fry, rounded to the nearest integer) for naturally spawning Glenariffe Stream chinook, 1965–90. Fry production for 1973–76 was estimated from trapping records; all other figures are based on a mean egg-to-fry survival of 48% (Unwin, 1997).

Brood year	Number of female spawners	Estimated fry production (thousands)	Number of returning adults	Adults per 10,000 fry
1965	1,278	2,988	4,676	16
1966	573	1,513	1,334	9
1967	746	1,760	505	3
1968	1,781	4,310	2,642	6
1969	1,286	3,249	2,760	8
1970	248	655	474	7
1971	1,084	2,573	330	1
1972	1,618	3,418	1,731	5
1973	160	275	3,207	117
1974	173	426	1,242	29
1975	799	1,834	2,045	11
1976	1,522	3,436	2,943	9
1977	778	1,614	1,341	8
1978	863	1,810	1,787	10
1979	1,413	2,138	546	3
1980	481	826	548	7
1981	856	1,978	1,097	6
1982	276	643	2,815	44
1983	326	784	1,766	23
1984	772	2,037	3,037	15
1985	1,800	4,722	950	2
1986	970	2,136	493	2
1987	669	1,400	1,151	8
1988	838	2,074	526	3
1989	391	767	615	8
1990	295	676	504	7

such as CV or skewness, which involve raising flows to the second and third power, respectively. I also calculated several indices related to the incidence of flood peaks, including the number of days when the daily mean discharge exceeded 500 m^3/s, 1,000 m^3/s, and 1,500 m^3/s, and the mean of the ten highest flows over the six months from August to January. The complete set of flow parameters used is summarized in Table 2.

For each parameter, I looked for evidence of a relation with the log-transformed Glenariffe Stream survival data by calculating the correlation coefficient for the paired data sets over the 26 years of record. I examined bivariate scatter plots and residual plots for any data sets showing a significant relation ($P<0.05$). For these preliminary results I did not correct for the effect of multiple tests (i.e. the possibility of finding an artificially inflated correlation with one of the 32 flow parameters purely by chance); therefore P-values for each correlation overestimated their true significance (Walters and Collie, 1988; Kope and Botsford, 1990). For these parameters, my next level of analysis was to recalculate the appropriate flow statistic for periods ranging in duration from one week to four months, dating from 1 June to 31 January (representing 805 periods in total), and to recalculate the correlation with the survival data for each choice of date and duration. I then constructed contour plots depicting variations in the correlation coefficient as a function of starting date and duration and examined these "surfaces of correlation" for the presence of local extrema. My motivation for this analysis was not to identify a single period that maximized the correlation, but rather to gauge the sensitivity of the correlation to small changes in interval, and hence to identify seasonal periods for which significant correlations between flow indices and survival persisted over biologically meaningful time scales.

All statistical calculations were performed with version 6.0 of SYSTAT software (Wilkinson, 1996). Contour and surface fits were accomplished with version 6 of SURFER for Windows' implementation of Kriging smoothing (Keckler, 1994) applied to a grid of correlation coefficients calculated at 5-day intervals on both the date and period axes.

Results

River flows

Over the period covered by this study (August 1965 to January 1991), monthly mean discharge ranged from 146 m^3/s to 306 m^3/s (Table 2). Individual

Table 2

Flow parameters used for correlation analysis, together with their mean and range over the period 1965 to 1990.

Parameter	Symbol	Mean	Range
Measures of flow volume (m^3/s)			
Mean annual flow, Feb–Jan	$\overline{Q}_{Annual}$	209	156–277
Mean flow, Aug–Jan	$\overline{Q}_{Spring/Summer}$	237	157–329
Mean flow, Aug–Oct	$\overline{Q}_{Spring}$	190	86–348
Mean flow, Nov–Jan	$\overline{Q}_{Summer}$	283	186–456
Mean flow, Aug	$\overline{Q}_{Aug}$	146	80–293
Mean flow, Sep	$\overline{Q}_{Sep}$	181	71–570
Mean flow, Oct	$\overline{Q}_{Oct}$	243	106–493
Mean flow, Nov	$\overline{Q}_{Nov}$	282	131–457
Mean flow, Dec	$\overline{Q}_{Dec}$	306	160–589
Mean flow, Jan	$\overline{Q}_{Jan}$	262	148–416
Measures of flood peaks (flows in m^3/s)			
Maximum flow, Aug–Jan	$\hat{Q}_{Spring/Summer}$	1,488	630–2,800
Maximum flow, Aug–Oct	$\hat{Q}_{Spring}$	975	167–2,470
Maximum flow, Nov–Jan	$\hat{Q}_{Summer}$	1,279	540–2,800
Maximum flow, Aug	$\hat{Q}_{Aug}$	385	86–2,470
Maximum flow, Sep	$\hat{Q}_{Sep}$	502	83–2,230
Maximum flow, Oct	$\hat{Q}_{Oct}$	755	133–2,030
Maximum flow, Nov	$\hat{Q}_{Nov}$	783	203–1,960
Maximum flow, Dec	$\hat{Q}_{Dec}$	1,006	282–2,800
Maximum flow, Jan	$\hat{Q}_{Jan}$	806	222–2,470
Mean of 10 highest flows, Aug–Jan	$\hat{Q}_{10max}$	854	443–1,410
Number of days $Q > 500$ m^3/s, Aug–Jan	N_{500}	13	3–26
Number of days $Q > 1{,}000$ m^3/s, Aug–Jan	$N_{1,000}$	2	0–8
Number of days $Q > 1{,}500$ m^3/s, Aug–Jan	$N_{1,500}$	1	0–4
Measures of flow variability			
Mean/median, Aug–Jan	$\tilde{Q}_{Spring/Summer}$	1.33	1.04–1.73
Mean/median, Aug–Oct	$\tilde{Q}_{Spring}$	1.32	1.01–1.92
Mean/median, Nov–Jan	$\tilde{Q}_{Summer}$	1.29	1.09–1.52
Mean/median, Aug	$\tilde{Q}_{Aug}$	1.14	0.98–2.25
Mean/median, Sep	$\tilde{Q}_{Sep}$	1.15	1.00–1.91
Mean/median, Oct	$\tilde{Q}_{Oct}$	1.22	0.94–1.64
Mean/median, Nov	$\tilde{Q}_{Nov}$	1.23	1.02–1.75
Mean/median, Dec	$\tilde{Q}_{Dec}$	1.27	1.04–2.11
Mean/median, Jan	$\tilde{Q}_{Jan}$	1.27	1.02–2.03

monthly means varied from 71 m^3/s (September 1977) to 734 m^3/s (December 1979). The mean maximum August to January flow (effectively the mean annual spring and summer flood) was 1,488 m^3/s; values for individual seasons ranged from 630 m^3/s in 1980 to 2,800 m^3/s in 1979. Flow variability was lowest during August and September, although highly variable flows ($\tilde{Q} > 1.6$) were recorded in all months.

Hydrographs for 1977 (a low-flow season) and 1984 (an above average season) illustrate the sharp peaks and rapid recession typical of Rakaia floods (Fig. 2). In the November 1984 event, discharge increased by a factor of 10 (from 172 m^3/s to 1,710 m^3/s) over 48 h and then fell from 1,960 m^3/s to 455 m^3/s over 72 h. Despite the contrast between the two seasons, both hydrographs also show a common period of low and relatively stable base flows in August and September, followed by more frequent floods as the season progresses.

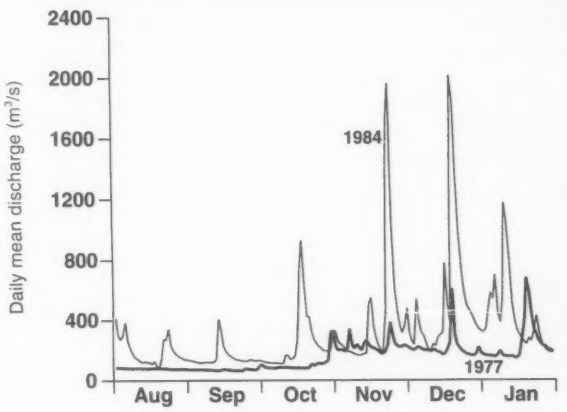

Figure 2

Rakaia River daily mean discharge (m^3/s) for spring and summer, 1977 and 1984.

Correlation analysis

Of the 32 flow parameters listed in Table 2, 29 showed no correlation with survival rates for Glenariffe Stream chinook (Table 3). Correlation coefficients for these indices ranged from –0.223 to 0.283, none of which differed significantly from zero ($P>0.16$ in all cases). The three exceptions were the mean flow $\overline{Q}$, the maximum flow $\hat{Q}$, and the ratio of the mean to median flow $\tilde{Q}$, for the month of November. All three measures were positively correlated with survival ($\overline{Q}_{NOV}$, $P = 0.045$; $\hat{Q}_{NOV}$, $P = 0.003$; $\tilde{Q}_{NOV}$, $P = 0.006$). By contrast, there was no correlation between survival and the same set of flow variables for the adjacent months of October and December.

The strongest and most consistent set of correlations involved the ratio of mean to median flow, calculated over periods of 30 to 90 d duration centered on or about November 1 (Fig. 3A). Over much of this range the correlation between $\tilde{Q}$ and log S exceeded 0.5, with a maximum value of 0.667 for $\tilde{Q}$ calculated over the 40-day period from 9 October to 17 November. More generally, survival tended to be high for broods corresponding to years when flow variability during October, November, and early December was high. For periods centered on the four weeks between

Table 3

Correlations between log-transformed brood year survival rates for Glenariffe Stream chinook and 32 indices of Rakaia mainstem flows, 1965–90. See Table 2 for definitions of symbols. Asterisks denote correlations significant at the 95% level (*) and 99% level (**).

	Flow parameter						
Period	$\overline{Q}$	$\hat{Q}$	$\tilde{Q}$	N_{500}	$N_{1,000}$	$N_{1,500}$	$\hat{Q}_{10max}$
February–January (year)	–0.091						
August–January (spring and summer)	–0.105	0.109	0.182	–0.062	0.261	0.165	0.164
August–October (spring)	–0.195	–0.140	–0.218				
November–January (summer)	0.046	0.205	0.269				
August	–0.068	–0.054	–0.066				
September	–0.082	–0.191	–0.159				
October	–0.223	–0.053	0.283				
November	0.397*	0.558**	0.520**				
December	–0.214	–0.112	–0.088				
January	–0.070	0.053	0.141				

18 October and 15 November, of five to nine weeks duration, the correlation between $\tilde{Q}$ and log S averaged 0.493. Taken as an isolated result, this correlation corresponds to an average significance level of $P < 0.01$ and an average coefficient of determination (r^2) of 0.243. There was some evidence of a weaker and more transient period of negative correlation between $\tilde{Q}$ and log S earlier in the season. For $\tilde{Q}$ calculated over periods of seven to nine weeks duration and centered on the fortnight from 6–19 September, the correlation with log S averaged –0.404, corresponding to an r^2 of 0.16. The symmetric upright "V" shape apparent in the contours of Fig. 3A, centered on the beginning of November, is an artifact caused by the tendency for data sets representing $\tilde{Q}$ over periods of similar duration centered on the same date to be highly correlated.

Maximum flow ($\hat{Q}$) and mean flow ($\overline{Q}$) were generally only weakly correlated with survival, and the few periods during which correlations stronger than ±0.4 were recorded showed little tendency to persist over temporal scales of more than a few days (Fig. 3, B and C). In addition, these correlations tended to become stronger at shorter time scales, suggesting that for $\overline{Q}$, and possibly for $\hat{Q}$, the correlations apparent in Table 3 were a transient effect of a fortuitous sequence of flood events. By contrast, the persistence of a positive correlation between $\tilde{Q}$ and log S for flows averaged over periods of up to 90 days suggests that the relation is much more robust and hence likely to be of biological significance. The correlations between $\overline{Q}$, $\hat{Q}$, and $\tilde{Q}$ are also consistent with this interpretation. Whereas $\overline{Q}_{NOV}$ and $\hat{Q}_{NOV}$ were highly correlated (r=0.84), $\tilde{Q}_{NOV}$ was only moderately correlated with both parameters (r=0.61 in both cases), confirming that $\tilde{Q}$ captured information on flow variation not measured by either $\overline{Q}$ or $\hat{Q}$.

The relation between $\tilde{Q}$ and log S was moderately influenced by the 1973 brood (for which the survival rate was unusually high) but was not dependent on it. The 1965, 1974, 1982, and 1983 broods (for which survival was also relatively high) and the 1985, 1986, and 1988

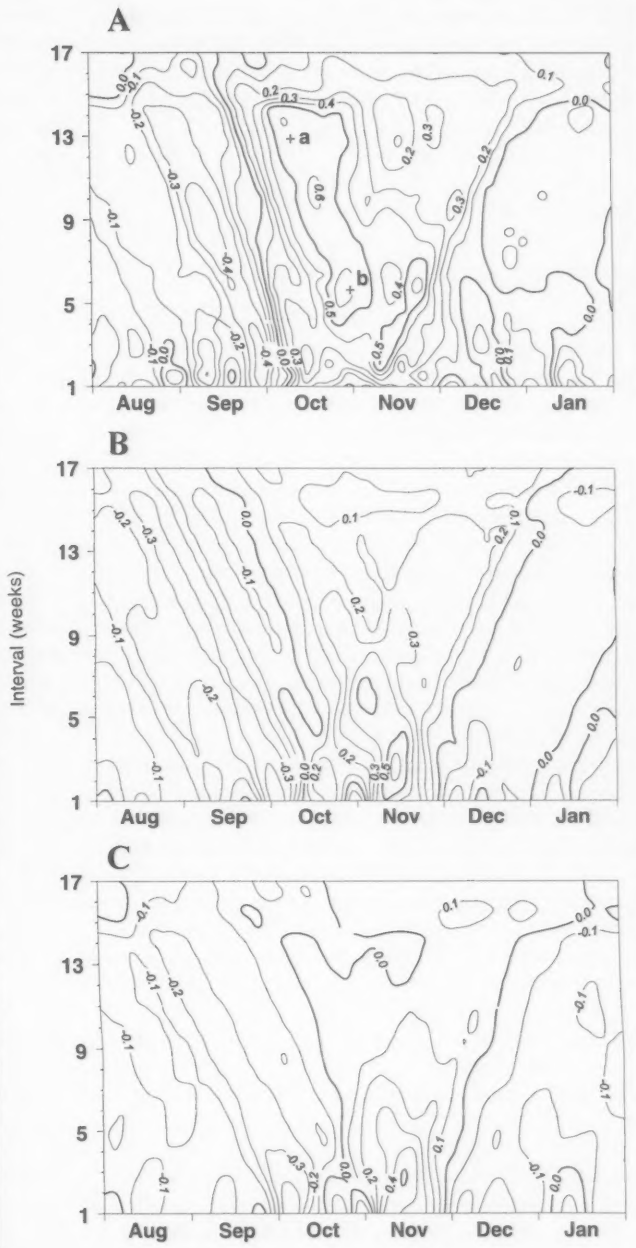

Figure 3

Correlations between log-transformed survival data for Glenariffe Stream chinook salmon and Rakaia River mainstem discharge expressed as the ratio of mean to median discharge (**A**), maximum discharge (**B**), and mean discharge (**C**), as a function of the period used to calculate each flow statistic. For each point, the locations on the x- and y-axes represent the mid-point of the period, and the duration, respectively. The points "a" and "b" correspond to the two intervals represented in Figure 4.

broods (for which survival was low) conform to the general trend irrespective of the duration of the period used to calculate $\bar{Q}$ (Fig. 4). With the exception of the 1969 brood, the value of $\bar{Q}$ during October and November was not highly sensitive to the choice of interval.

Discussion

Correlations and flow parameters

This study shows that, although fry-to-adult survival of Glenariffe Stream chinook salmon is correlated with the occurrence of springtime flood events in the Rakaia River, both the magnitude and the direction of the observed correlation depend strongly on the flow parameter used and the period over which this parameter is calculated. Survival was most strongly correlated with flow variability (as measured by the ratio of mean to median flow), the correlation being moderately negative for flows averaged over the period from mid-August to mid-October, and rather more strongly positive from mid-October to November. Similar but weaker correlations were apparent between survival and maximum flow, but mean flow was a poor predictor of survival irrespective of the time interval used.

The correlations reported here have two key features. First, although quite strong in a biological context, they are nevertheless relatively weak, accounting for at most 25–30% of the observed variation in log survival. Even if the maximum positive correlation (r=0.667) is taken at face value, its predictive power allows years to be categorized only as "above average" or "below average," at best (Prairie, 1996). This result is consistent with an earlier finding that annual survival rates for New Zealand chinook are primarily determined by marine rather than freshwater influences (Unwin, 1997; see also Bradford, 1995). Second, the tendency for survival to be positively correlated with flow variation but uncorrelated with mean flow suggests that increased flow variability (in the sense illustrated in Fig. 5) at the appropriate time of year is beneficial to survival. This is in sharp contrast to the generally held view that spring floods have a detrimental impact on chinook fry in the Rakaia and other New Zealand rivers (Waugh, 1980; McDowall, 1990; Flain[1]).

The three key flow parameters used in this study—mean flow, maximum flow, and ratio of mean flow to median flow—are by no means the only ones possible and can only capture some of the information contained in the hydrograph for a given time period. Mean flow essentially measures the total volume of water passing through the river over the interval in question, without conveying any information about the magnitude or distribution of floods. For example, a 90-day mean of 200 m^3/s could arise from 90 consecutive days at exactly 200 m^3/s each, or from 89 days at 180 m^3/s and one day at 1,980 m^3/s. Maximum flow characterizes peak flood intensity, but not flow variability, so that a flow period with one 2,000 m^3/s flood will outrank another period with ten 1,900 m^3/s floods.

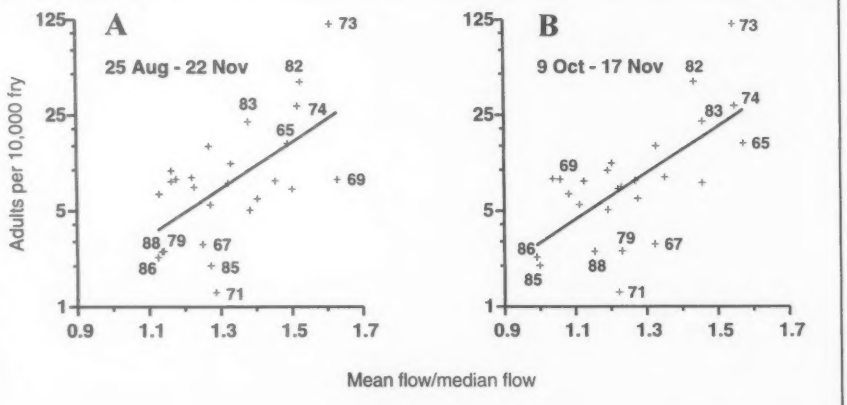

Figure 4

The relation between log-transformed survival data for Glenariffe Stream chinook salmon and the ratio of mean to median discharge in the Rakaia River mainstem for two periods near local maxima in Figure 3A. Twelve points corresponding to broods with extreme survival or flow indices for at least one of the two periods shown are identified by year.

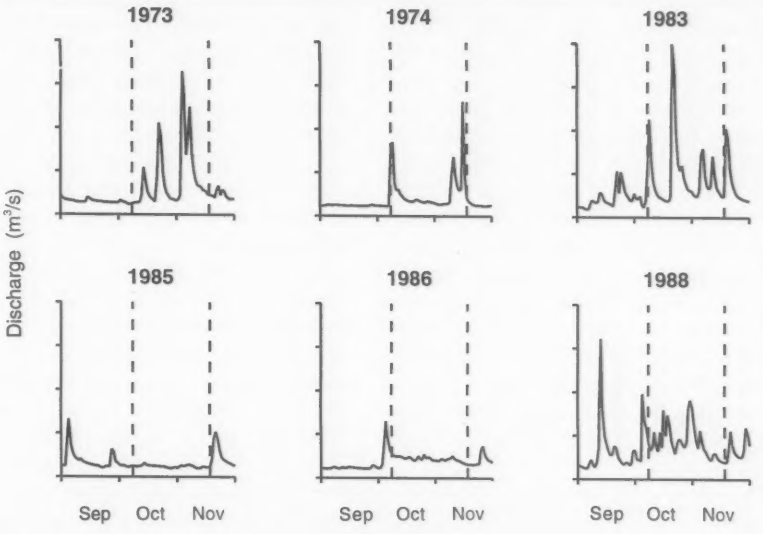

Figure 5

Hydrographs for the Rakaia River from September to November for three years of high mean flow to median flow (as calculated over the period indicated by dashed lines) and high survival (1973, 1974, 1983) and three years of low mean flow to median flow and low survival (1985, 1986, 1988). All hydrographs are drawn to a common vertical scale of 0–2,000 m^3/s.

The ratio of mean to median flow is a direct measure of flow variability, but it does not necessarily follow that low values of $\tilde{Q}$ correspond to low and stable flows. Flow regimes where $\tilde{Q}$ is close to one (i.e. mean flow differs little from the median) can arise in two different ways, only one of which corresponds to an extended period of low flows (Fig. 5). The other possibility is a period of highly variable flows superimposed on a high base flow, so that even though flows vary greatly from day to day, the flow distribution is only moderately skewed. By contrast, high values of $\tilde{Q}$ are more consistently associated with highly variable flows, tending to correspond to intervals when a lengthy period of low, stable base flows is punctuated by a relatively small number of short and sharp flood events. Both the 1973 and 1974 seasons ($\tilde{Q}_{9\ Oct-17\ Nov}$=1.54 and 1.55, respectively) were characterized by low and stable base flows during September, followed by two or three relatively short-lived flood events during October and November. The 1985 and 1986 seasons ($\tilde{Q}_{9\ Oct-17\ Nov}$=1.00 in both cases) were characterized by uniformly low and stable flows, with no floods over the six weeks from 1 October. The effect of high base flows on flow variability is illustrated by comparing the 1983 and 1988 seasons ($\tilde{Q}_{9\ Oct-17\ Nov}$=1.46 and 1.15, respectively). Whereas base flows were low throughout 1983, so that a 2,000 m^3/s event in late October generated a high figure for $\tilde{Q}$, the absence of a major flood during October and November 1988 produced a lower figure for $\tilde{Q}$ despite high and rapidly fluctuating base flows over most of the period shown.

The other flow parameters examined during the initial phase of this study, such as the number of days from August to January when flows exceeded a certain level, showed no correlation with survival. Although in principle it would have been possible to subject these parameters to the same level of analysis used for $\bar{Q}$, $\hat{Q}$, and $\tilde{Q}$, this analysis becomes progressively less meaningful at shorter time scales. For example, given that $N_{1,000}$ ranged from 0 to 8 over a six month period (Table 2), the same statistic calculated over monthly intervals would typically take on only a few discrete integer values and would be inappropriate for correlation analysis.

Mechanisms

The topography of the correlations between $\tilde{Q}$ and survival, as illustrated by the qualitative features of Fig. 3A, coincides to a striking degree with several key events in the migration patterns of juvenile ocean-type fry in the Rakaia River. The period of highest positive correlation between flow variability

and survival, mid-October to November, coincides with the period when fingerlings first become abundant in the lower river and begin their transition to oceanic waters. The period centered on mid-September, when there is some evidence of a negative correlation between flow variability and survival, corresponds to the earlier time when fry are still migrating downriver and have yet to grow to the point where they are able to withstand the transition to salt water. Survival is not correlated, either positively or negatively, with flow variability at the beginning of the season (August, when most fry have yet to hatch) or at the end of the season (January, by which time most fingerlings have left the river). The correlation also tends to disappear when flow variability is averaged over more than about 100 days, a period that is consistent with the 90-day freshwater residence period of Rakaia fingerlings.

The tendency for survival to be positively correlated with flow variability rather than flow volume (as measured by $\overline{Q}$), and the short duration of each individual flood peak, suggest that these flood pulses must be an integral part of any plausible linking mechanism. Maximum survival appears to result when stable flows prior to mid-October are followed by a few (perhaps two or three) large floods over the next four to six weeks. By contrast, seasons when there are no major floods during October and November seem to result in poor survival irrespective of flows earlier in the season. Although any discussion based solely on the present results is speculative, I suggest that sudden increases in Rakaia discharge coinciding with peak emigration of fingerlings from the river mouth may increase survival by buffering the transition from fresh to saline waters in the vicinity of the offshore plume. If so, these pulses may help to compensate for the lack of an estuary at the Rakaia mouth and the low importance of the lagoon as a salmon rearing habitat,[2] one of the key features distinguishing the Rakaia (and other New Zealand salmon-producing rivers) from the extensive tidal basins below the Sacramento River mouth (Kjelson et al., 1982). The effect may be compounded by the well-documented tendency for downstream migration rates to increase with flow, both in New Zealand (Irvine, 1986) and North American populations (e.g. Kjelson et al., 1982; Berggren and Filardo, 1993), so that each flood pulse increases both the number of fingerlings leaving the river and their prospects for successful acclimation to salt water. Outflow of turbid flood waters may also increase survival by reducing visibility, and hence decreasing losses to inshore marine predators such as kahawai (*Arripis trutta*), although reduction in visibility is likely to be no more than a secondary effect (cf. St. John et al., 1992). A positive correlation between survival of hatchery-reared Atlantic salmon (*Salmo salar*) and maximum river discharge during the first seven days after release has been attributed to reduced predation at higher flows (Hvidsten and Hansen, 1988).

A distinguishing feature of chinook salmon compared with other species of *Oncorhynchus* is their gradual acquisition of seawater tolerance while still in fresh water, without the sudden transition associated with smoltification in species such as coho (*O. kisutch*) or steelhead (*O. mykiss*) (Hoar, 1976). By early November, Rakaia fingerlings are of an age and size close to the generally accepted minima for successful transfer to seawater (Clarke and Shelbourn, 1985; Franklin et al., 1992), and water temperatures in the Rakaia River (12–15°C; Unwin, 1986) and at sea (12–14°C)[8] appear to be within the optimal range for juvenile chinook salmon reported by these studies. However, acclimation to seawater also depends on the rate of transition. A gradual transfer to saline waters allows even very young fish to acclimatize successfully (Hoar, 1976), as evidenced by the abundance of chinook fry in low salinity estuarine waters in North America (Reimers, 1973; Healey, 1980; Levy and Northcote, 1981), including the lower Sacramento River (Kjelson et al., 1982). Changes in estuarine ecology during low-flow seasons in the Snake-Columbia River system have been suggested as a factor contributing to reduced survival of Snake River chinook (Williams and Matthews, 1995). In the Strait of Georgia, where the Fraser River plume forms a well-developed halocline at a depth of 5–10 m, juvenile salmonids showed a preference for surface waters of low salinity (10–15 ppt) in the plume, compared with the more saline waters (25–30 ppt) in other regions of the Strait (St. John et al., 1992). The Georgia Strait study also reported a tendency for plankton and larval fish to align with the plume boundary, providing enhanced feeding opportunities.

There have been no studies on salinity gradients off the Rakaia mouth, but nearshore salinity off Otago Harbour (on the east coast of the South Island 220 km south of the Rakaia) is inversely correlated with discharge from the Clutha River a further 100 km to the south (Jillett, 1969). The coastal shelf off the Rakaia River has a very gentle slope, with the 20-m isobath 5–10 km offshore (see Fig. 1). Consequently, peak Rakaia outflows should have a substantial impact on inshore salinity. For example, a daily mean discharge of 1 200 m^3/s over 24 h (which is less than the mean annual spring flood) represents a total volume of fresh water of 0.1 km^3, equivalent

[8] 1997. NIWA, Christchurch, New Zealand. Unpubl. data.

to a 10 km^2 surface layer that is 10 m deep. Devolvement of the resulting halocline would presumably require considerable input of wave energy, and under calm conditions, a surface layer of low salinity water may persist for some days until dispersed to the north-east under the influence of the Southland current (Heath, 1972).

Implications

The analysis described in this study relates only to ocean-type fry. Because ocean-type fish make up approximately two thirds of the Rakaia adult population (Quinn and Unwin, 1993), fluctuations in their abundance would have a significant impact on brood year survival. However, one third of Rakaia adult chinook have a stream-type juvenile life history, and there is some evidence that the emergence of stream-type behavior in what was originally a fall-run stock represents an adaptive response to the lack of estuarine waters on New Zealand's salmon-producing rivers (Unwin and Glova, 1997). The freshwater habitat preferences and migration patterns of stream-type chinook in the Rakaia River are poorly understood, and their sensitivity to flow variations is unknown. However, the possibility that survival of ocean-type fry may increase in seasons of variable flow could provide a compensating selective force that would help to establish a balance between the incidence of the two phenotypes. If so, the ratio of ocean- to stream-type fry in any one annual cohort should also be positively correlated with the variability of spring flows into the Rakaia River during the first year of life.

To explore this hypothesis further, and hence to provide an independent test of the plausibility of the mechanisms outlined in the previous section, I examined archival material from NIWA's scale collections, aspects of which are summarized in Tables 2, 3, and 4 of Quinn and Unwin (1993). These records include scale samples from salmon taken in the Rakaia sports fishery for nine annual cohorts between 1965 and 1984. These scale samples permitted returning fish from each cohort to be classified according to juvenile life history. The incidence of ocean-type fish among 3-year-old adult chinook was positively correlated with mainstem flow variability over the period 9 October to 17 November (r^2=0.54, P=0.025; Fig. 6) during the year in which they emigrated as juveniles. Of particular interest is the high incidence of ocean-type fish in the 1973 and 1982 cohorts, which were also the broods for which survival was highest.

With regard to the New Zealand salmon fishery, which is managed purely for recreational anglers

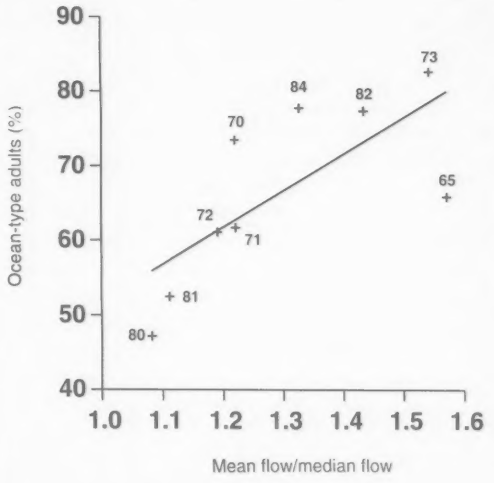

Figure 6

The relation between the incidence of ocean-type adults among 3-year-old chinook salmon caught by Rakaia River anglers over nine seasons from 1965 to 1984, and the ratio of mean to median discharge in the Rakaia mainstem for the corresponding juvenile cohort, for the same time interval (9 October to 17 November) as that represented in Figure 4B. Sample sizes averaged 127, and ranged from 36 to 373.

(McDowall, 1994b), the main conclusion to be drawn from this study is that despite the observed correlations between survival and flow variability, interannual variation in survival remains at best weakly predictable. However, spring flow variability is easy to analyze on a season by season basis, and the possibility of making at least a broad prediction identifying years of high or low survival up to two seasons in advance suggests the effort is worth making. The New Zealand Fish and Game Council (which is responsible for management of the sports fishery) have recently instituted annual monitoring programs for key spawning runs in all major salmon rivers,[9] and these will eventually enable comparisons between survival and flows to be made for other major east coast catchments. My results also suggest that any reduction in flow variability resulting from development of storage impoundments for hydroelectric or irrigation purposes would have a significant negative impact on the fishery over and above any losses caused by barriers to upstream passage. The high bed load of major braided rivers such as the Rakaia makes them unattractive candidates for impoundment, but declines in salmon runs in two other riv-

[9] Webb, M. 1997. Central South Island Fish and Game Council, PO Box 150, Temuka, New Zealand. Personal commun.

ers (the Clutha and Waitaki) following hydroelectric development (McDowall, 1990) may be partly linked to a reduction in the magnitude and frequency of spring floods. A positive association between salmon production and large offshore plumes is also consistent with the general distribution of salmon in east coast rivers (McDowall, 1990), with the largest populations confined to major rivers draining the main divide. Traditionally this distribution has been attributed to the presence of stable headwater spawning tributaries such as Glenariffe Stream, but this explanation is not fully convincing. Many minor east coast rivers support self-sustaining stocks of brown trout (Jowett, 1990; McDowall, 1990), and spawning requirements for chinook are not dissimilar.

From an evolutionary standpoint, the present results help to shed further light on the processes by which chinook salmon have been able to succeed in New Zealand waters. In addition to the emergence of stream-type fish as a significant component of modern New Zealand stocks, several other recent studies have noted differences between present-day New Zealand and Sacramento chinook at both phenotypic and genotypic levels (Quinn and Unwin, 1993; Quinn et al., 1996), suggesting that the process of adaptation may be ongoing. The somewhat unusual mechanisms which have apparently enabled New Zealand chinook salmon to establish the only self-perpetuating stocks outside their native range (Harache, 1992) underscore the great phenotypic plasticity of the species, and the value of the New Zealand populations as a laboratory for studying this plasticity.

Acknowledgments

I thank all staff associated with the Glenariffe programme for technical assistance; Greg Kelly and Mark Weatherhead for help with drafting the figures; Bob McDowall, Charles Pearson, Ian Jowett, Tom Quinn, and three anonymous referees for comments on earlier drafts of the manuscript. Kathy Walter and Graeme Davenport extracted Rakaia River flow data from the National Water Resources Archive, and the study was funded by the Foundation for Research, Science and Technology through Contracts CO1417 and CO1501.

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A shift in distribution of humpback whales, *Megaptera novaeangliae*, in response to prey in the southern Gulf of Maine

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Abstract.—From the mid-1970's to the mid-80's, Stellwagen Bank was an important humpback whale feeding area with sand lance (*Ammodytes* spp.) as the major prey. Between 1988 and 1994, however, the number of humpback whales we identified each year on Stellwagen declined from a high of 258 (1990) to 7 (1994), and the mean number of whales identified per day fell from 17.7 (1988) to 0.9 (1994). Adult whales decreased steadily after 1988; juveniles decreased rapidly after 1991. Echo-sounder data from Stellwagen showed that prey trace levels declined from 19.1% of the vertical water column in 1990 to 2.8% in 1992 (no readings were taken in 1988–89, or 1993–94). Simultaneously, the number of whales identified on Jeffreys Ledge, north of Stellwagen Bank, increased dramatically beginning in 1992. Sixty-four percent of the whales identified on Jeffreys in 1992–94 were seen on Stellwagen Bank in 1988 and 1989. We hypothesize that humpback whales shift their distribution in order to prey upon recovering herring populations, their primary source of food.

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Fishery Bulletin 95:826–836 (1997).

Humpback whales, *Megaptera novaeangliae*, migrate seasonally between low-latitude breeding grounds and high-latitude feeding areas (Kellogg, 1929; Mackintosh, 1965; Katona, 1986). In the western North Atlantic, whales that winter in Caribbean waters migrate to feeding grounds in New England (the Gulf of Maine), in the Gulf of St. Lawrence, and in waters off Newfoundland, Greenland, Iceland, and Norway (Katona and Beard, 1990). The whales using each feeding area appear to consist of extended matrilines (Baker et al., 1990; Clapham et al., 1992). Within feeding areas, prey distribution has been a primary influence on the local distribution and micromovements of all baleen whales examined to date (Whitehead and Carscadden, 1985; Payne et al., 1986, 1990; Piatt et al., 1989).

Studies of humpback whale movement, ecology, demography, behavior, and social organization on their feeding grounds in the Gulf of Maine have been ongoing since the mid-1970's, (Payne et al., 1986; Clapham and Mayo, 1987, 1990; Weinrich, 1991; Weinrich and Kuhlberg, 1991; Clapham et al., 1992; Weinrich et al., 1992; Katona et al.[1]). During this period, several shifts in the distribution of humpback whales have been reported. Payne et al. (1986) showed that humpback whales in the late 1970's had moved from primary abundance on Georges Bank and in the waters of the northern Gulf of Maine to the inshore southwestern Gulf of Maine, especially Stellwagen Bank and the Great South Channel. They attributed this shift to a fishery-induced collapse of herring (*Clupea harengus*) populations (Anthony and Waring, 1980; Grosslein et al., 1980) and a corresponding increase in sand lance (*Ammodytes* spp.) (Meyer et al., 1979; Sherman et al., 1981, 1988; Sherman 1986; Sissenwine 1986). Both species are known prey for humpback whales (Mitchell, 1973; Overholtz and Nicholas, 1979; Kawamura, 1980). These fish species are potential ecological competitors (Reay, 1970; Meyer et al., 1979; Sherman et al., 1981); moreover, herring are known predators of

[1] Katona, S. K., P. Harcourt, J. S. Perkins, and S. D. Kraus. 1980. Humpback whales: a catalog of individuals identified by fluke photographs. College of the Atlantic, Bar Harbor, ME, var. pagination.

sand lance (Fogarty et al., 1991). Sightings of humpback whales off the Maine coast, where herring were the primary whale prey, decreased dramatically during the late 1970's (Payne et al., 1986; Mullane and Rivers[2]). Sand lance frequently use shallow areas with sandy bottoms, such as Stellwagen Bank in the southern Gulf of Maine (Meyer et al., 1979). This shift in distribution, and corresponding change in primary prey type, may have also led to changes in feeding behavior (Weinrich et al., 1992). Humpback whales remained abundant in the southwestern Gulf of Maine throughout the 1980's, with a brief decrease in some areas during 1986–87 (Payne et al., 1990; Cetacean Res. Unit[3]).

We documented a gradual but continuous decrease in the use of Stellwagen Bank by humpback whales during 1988–94. Our data suggest that whales have returned to a distribution similar to that documented until the late 1970's. We hypothesize that this return is due to the recovery of herring stocks in the Gulf of Maine and to a corresponding decrease in available prey for humpback whales on Stellwagen Bank and in other areas favored by sand lance in the southwestern Gulf of Maine.

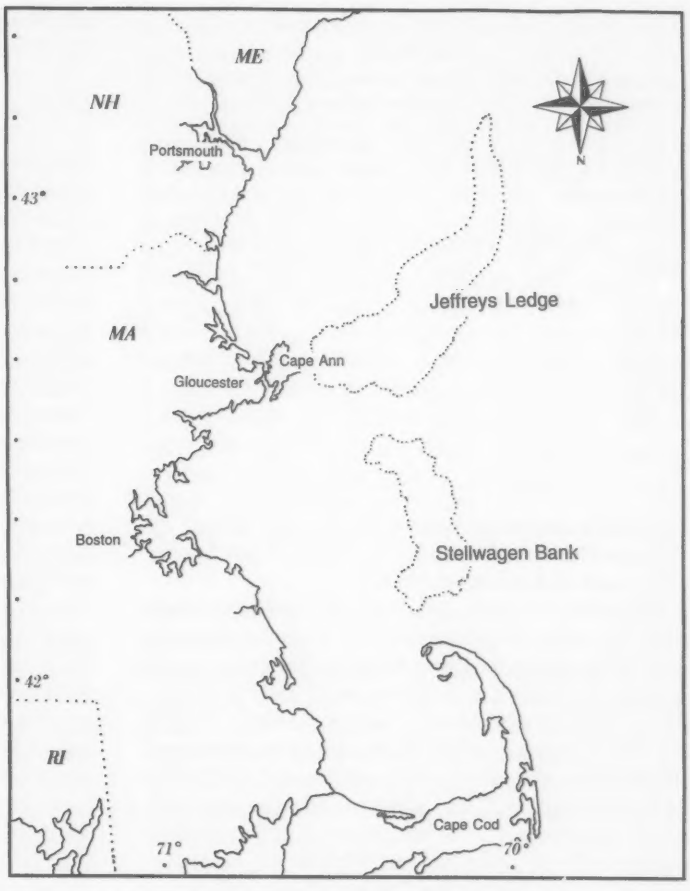

Figure 1
The study area in the Gulf of Maine.

Methods

Survey methods

From 1 May to 30 October, 1988 to 1994, daily shipboard surveys were carried out aboard commercial whale-watching boats. These departed from Gloucester and Boston, Massachusetts, and were typically 4–5 hours in duration. There were usually two cruises per vessel per day. A typical cruise included 90–120 minutes in areas where whales were often observed, as well as 2–3 hours of transit time. Whale watches usually emphasized the northern half of Stellwagen Bank. On occasion, whale watches surveyed the southern half of Jeffreys Ledge to the northeast of Cape Ann (Fig. 1). This effort is detailed in Table 1. Within each whale-watching trip, protocol and typical amount of observation time were consistent on all vessels.

Whale-watching cruises were supplemented by occasional day-long (7–13 h) excursions on research vessels. These took place 1 April to 15 November of each year, with emphasis on April and October–November, as well as during periods of significant whale concentration from May to September. During each cruise, a specific attempt was made to conduct a comprehensive photo-identification survey of a specific area (i.e. northern Stellwagen Bank, southern Jeffreys Ledge, etc.). As time allowed, coverage was devoted to a larger portion of the entire geographic feature (either Stellwagen Bank or Jeffreys Ledge). Specific areas were determined by recent sightings of whale aggregations, reliable reports of whale sightings from local boaters, or a determination that an area had not been recently surveyed. Jeffreys

[2] Mullane, S. J., and A. Rivers. 1982. Mt. Desert Rock, Maine. Annual Report, 27 p. [Available from Allied Whale, College of the Atlantic, Bar Harbor, ME.]

[3] Cetacean Research Unit. 1980–89. Cetacean Research Unit, PO Box 159, Gloucester MA 01930. Unpubl. data.

Table 1

Study effort by both number of survey days and number of survey trips for both Stellwagen Bank and Jeffreys Ledge. "JLSN days" represent the total number of survey days represented by the Jeffreys Ledge Sighting Network (JLSN), established after the 1992 season (see text for further details).

Year	Stellwagen days	Stellwagen trips	Jeffreys days	Jeffreys trips	JLSN days
1988	145	558	16	44	0
1989	151	550	17	20	0
1990	166	516	32	37	0
1991	160	460	31	36	0
1992	171	506	34	37	69
1993	106	364	48	79	119
1994	86	141	86	141	138

Ledge was the destination for just under half of the dedicated cruises from 1988 to 1992, all but four in 1993, and all but two in 1994.

Beginning in 1990, sighting and photo-identification data were also collected from a whale-watching boat operating out of Kennebunk, Maine, to obtain information from the northern end of Jeffreys Ledge. Observer coverage was for one trip per day, 3–5 days per week. Because of the unusually large number of whales first observed on our dedicated cruises to Jeffreys Ledge in 1992, a photo-identification network (consisting of three whale-watching boats working on Jeffreys Ledge for one trip per day) was formalized in fall 1992 (after the completion of field efforts), and existing 1992 data were obtained. Beginning in 1993, data collection from these vessels was standardized to be directly comparable with Stellwagen Bank whale-watching data. Because 1993 represented the first year in which Jeffreys Ledge data were collected in any kind of standardized fashion, occurrence and occupancy (defined below) were not calculated for Jeffreys Ledge humpback whale sightings.

Study areas

Stellwagen Bank, now a National Marine Sanctuary, is a sandy glacial deposit approximately 32 km long with depths from 18 to 37 m (Fig. 1). It borders the eastern margin of Massachusetts Bay and is located approximately halfway between Cape Ann and Cape Cod, Massachusetts. Jeffreys Ledge is a more complex, winding, shallow ledge, with typical depths of 45 to 61 m and with a length of approximately 54 km. Its substrate is a mixture of rocky and muddy bottoms. The southern edge of Jeffreys Ledge is 9 km northeast of Rockport, Massachusetts, whereas the northern end lies 36 km east of York, Maine. Stellwagen Bank and Jeffreys Ledge are separated by 21.6 km at their closest point.

Field methods

Individual humpback whales were identified from photographs of distinctive pigment patterns on the ventral surface of their tail flukes or from the shape of and scarring on the dorsal fin (or by both features) (Katona and Whitehead, 1981). Two observers collected data on each whale or group of whales. One observer was responsible for photographing each whale, while the second recorded the whale's location (by means of LORAN-C), group affiliations, and behavior. This observer also recorded which photographs were taken of each whale, as dictated by the photographer. Each group of whales in an area was usually observed for 1–30 minutes; most, if not all, whales in a single location (3–5 km radius) were identified during each observation period. Field methods were consistent on all vessels.

Age class and sex determination

Individuals were identified by comparing photographs with those of a catalog of humpback whales maintained at the Cetacean Research Unit (CRU), Gloucester, MA. Details on cataloging methods and contents of the catalog were given in Weinrich (1991), Weinrich and Kuhlberg (1991), and Weinrich et al. (1992) and are based on procedures outlined by Katona and Whitehead (1981). Whales were sexed by photographing them while belly up at the surface (and by noting the presence or absence of a small lobe immediately posterior to the genital slit [Glockner, 1983]), by observing a female with calf, or by using molecular techniques (Baker et al., 1991). Individuals were assigned to age classes (juvenile or adult) based on known age (first observation as a calf) or based on the consensus among all experienced CRU observers of an animal's relative size at first sighting. The accuracy of the latter technique was confirmed by estimating the age class of animals of unknown identity in the field and by finding that these estimates matched (photographically) animals of known age. No incorrect classifications were made (n=51). For the purposes of this paper, an animal was classified as an adult if it was known to be at least five years old, an age at which 50% or more of the population is mature (Chittleborough, 1965; Clapham and Mayo, 1990).

Prey density

In 1990–92, a SITEX HE-358 50-kHz echo-sounder and chart recorder aboard a whale-watching vessel

were used to record prey density on Stellwagen Bank in the immediate area where whales had been observed. The echo-sounder was used for 83 days during 1990 (9 May to 20 October; 153 total hours), 98 days during 1991 (9 May to 28 September; 221 total hours), and 69 days during 1992 (24 April to 24 October; 60 total hours). Clear readings throughout the water column (i.e. with no interference present) were obtained for 69 hours in 1990, 166 hours in 1991, and 60 hours in 1992. An echo-sounder operating at this frequency is likely to detect the presence of fish but unlikely to detect plankton unless it is present in extreme densities (Dolphin[4]). The echo-sounder was started as the boat slowed to begin whale observations and turned off when the vessel left the observation area to return to port. Because echo-sounder tracings were obscured by noise when the vessel was moving at cruising speed (e.g. moving from one group of whales to the next), tracings performed at cruising speed were eliminated from analysis. A timing mark was placed simultaneously on both the echo-sounder chart and the data sheets by the second observer at 10-min intervals.

The echo-sounder chart was later sampled at 2-min intervals by interpolating between the 10-min marks. For each sampling point, prey presence was scored visually in 3.3 m (10 ft) vertical increments from the surface to the bottom, with a sliding score of zero (for no prey) to 10 (prey throughout that 3.3 m interval). From these readings mean values for vertical bait density were calculated for each quarter of the water column and the total water column. Mean depth in which readings were taken was 38.4 m (SD=15.1 m). No echo-sounder data were recorded on Jeffreys Ledge.

Although such data give an idea of the availability of prey in the immediate vicinity of whales, they do not reflect an area where whales were not present. Hence, there could have been very similar or different prey concentrations very nearby, without that information ever being recorded. However, since each year's data set came from numerous days and contained data points from several different locations (albeit within a 3–4 mile radius) within each day's observations, we feel they at least give a crude overview to overall prey densities in the vicinity of whales.

Data management and analysis

Both daily whale sighting data and prey density data were stored in PC-based computer files and analyzed with commercially available statistical software (SPSS/PC+, Kinnear and Gray, 1992). For daily sighting data, an Xbase program was written to isolate the sightings of each whale and to calculate statistics summarizing that individual's within-year sighting history (including occurrence and occupancy—see below) in each part of the study area. These values were then stored in a separate data file and analyzed with the same statistical software. Temporal trends were analyzed with least-squares regression (Snedecor and Cochran, 1967) of individual data points with the year of observation as the independent variable, although only annual means are presented in our tables for occurrence and occupancy scores. The slope of the regression line (B) and the probability value (P) from a test of the null hypothesis that the slope did not differ from zero are presented for each test. Calves were eliminated from these analyses because we assumed that a calf is merely following the mother in her choice of habitat.

Definitions

"Occurrence" is defined as the number of days on which an individual whale was photographed in a single year. "Occupancy" is the number of days elapsed from the first to the last recorded sighting of an individual whale within a year. These definitions are consistent with those used by Clapham et al. (1992).

Results

Stellwagen Bank

Total number of humpback whales identified per year The number of humpback whales identified in any single year on Stellwagen Bank ranged from 258 (1990) to a low of 7 (1994), with a mean of 153.6 (SD=88.4) (Fig. 2). These values show a statistically significant declining trend (B=–32.82, P=0.033).

When the total number of whales was broken into age class, differences in annual trends were apparent. Numbers of adult whales identified on Stellwagen ranged from 173 (1990) to 3 (1994; mean=102.8, SD=60.4). These values also showed a statistically significant declining trend (B=–0.84, P=0.018). Number of juveniles identified in each year varied from 85 (1990) to 4 (1994; mean=50.71, SD=29.2). These also showed a downward trend, although not statistically significant (B=–23.50, P=0.099). The ratio of identified adult whales to identified juveniles varied from 2.5:1 (in 1988) to 0.75:1 (in 1994). Numbers of cow-calf pairs throughout the study period

[4] Dolphin, W. F. 1994. Department of Biomechanical Engineering, Boston University, Boston, MA 02215. Personal commun.

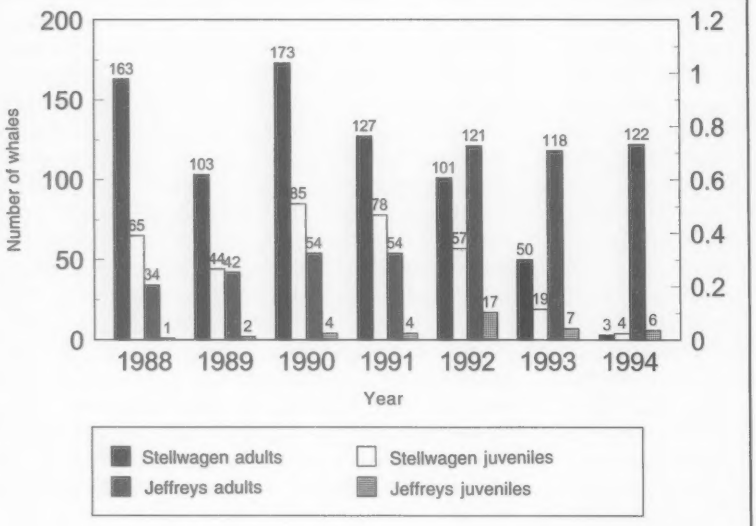

Figure 2

The number of individual humpback whale adults and juveniles identified per year on Stellwagen Bank and Jeffreys Ledge, 1988–94. Note the rapid annual decrease of adults on Stellwagen Bank starting in 1991, and the corresponding increase on Jeffreys Ledge beginning in 1992. Juveniles started a rapid decrease on Stellwagen Bank in 1992.

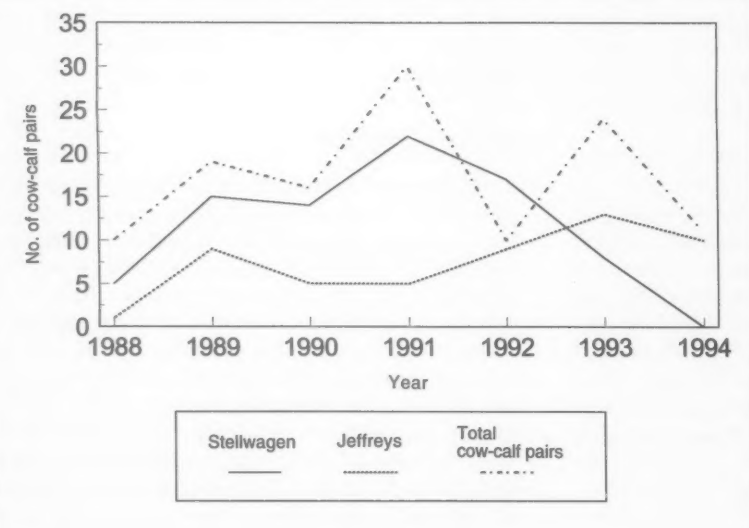

Figure 3

The number of cow-calf pairs on Stellwagen Bank, Jeffreys Ledge, and in the entire Gulf of Maine, 1988–94. The percentage of known mother-calf pairs that were sighted on Stellwagen began to decrease dramatically in 1992, the same year that the percentage mother-calf pairs began to increase on Jeffreys Ledge.

showed no significant trend in the absolute number seen on Stellwagen (B=–1.214, P= 0.424). Numbers of cows and calves began in 1991 to decline sharply, especially when compared with the total number of cow-calf pairs in the Gulf of Maine. By the last year of the study no cow-calf pairs were seen (Fig. 3).

Occurrence and occupancy

Mean occurrence of humpback whales on Stellwagen Bank within a single season ranged from 13.1 days (1989, n=147) to 6.6 days (1993, n=69) (Table 2; B=–0.30, P=0.501). Adults showed a within-year mean occurrence of 6.4 days (SD=4.8, n=720), with a statistically significant declining trend through the study period (B=–1.98, P<0.001). Compared with adults, juveniles showed a higher mean within-year occurrence (mean= 14.5 days, SD = 4.2, n=352), which significantly increased throughout the study period (B=1.63, P=0.030).

Occupancy of individual whales within years declined significantly from a mean of 61.8 days (1989, n=147) to 21.6 days (1994, n=7) (Table 3; B=–7.07, P=0.002). Again, age classes showed different trends. Adults had a mean occupancy period of 39.3 days (SD = 23.56, n=720) throughout the study period, with a significant declining trend (B=–10.65, P<0.001). In contrast, juveniles had a mean occupancy period of 55.0 days (SD=13.21, n=352), with no significant trend apparent (B=–2.82, P=0.296).

Although juveniles showed no significant trend in occupancy and had occurrence values that actually increased throughout the period, a comparison of median values for

Table 2

The mean occurrence (in days) of humpback whales on Stellwagen Bank, 1988–94.

Year	Adults	Juveniles	Combined total
1988	13.5	7.2	11.2
1989	12.2	15.2	13.1
1990	7.9	12.5	9.6
1991	6.2	17.0	10.7
1992	7.2	19.6	12.0
1993	3.1	15.7	6.6
1994	1.3	19.8	11.9

Table 3

The mean occupancy (in days) of humpback whales on Stellwagen Bank, 1988–94.

Year	Adults	Juveniles	Combined total
1988	67.9	47.1	60.4
1989	56.5	71.6	61.8
1990	52.3	55.0	51.8
1991	47.5	73.1	54.6
1992	32.4	53.3	42.2
1993	17.2	48.4	25.7
1994	1.3	36.8	21.6

each of these variables portrays a trend more similar to that seen from adults. From 1992 through 1994, prolonged residency of a few juveniles skewed occurrence and occupancy values. During 1991–93, median occurrence of juveniles fell from seven days to three, whereas median occupancy periods fell sharply, from 59.5 days to 15 days. In 1994, so few juveniles were seen (four) that the relatively high values of two individuals severely skewed the results for that year. Median values of adult occurrence and occupancy showed the same trends as those portrayed from the regression analyses.

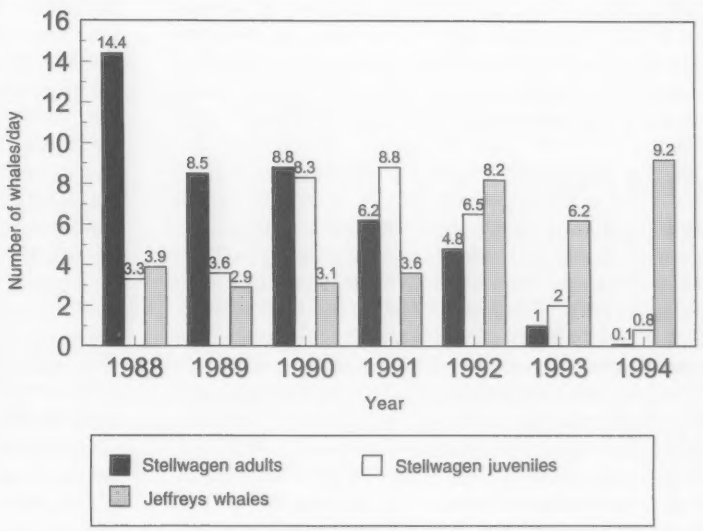

Figure 4

The mean number of whales identified per day in each age class and year on Stellwagen Bank and Jeffreys Ledge, 1988–94. Jeffreys Ledge juveniles were not included because of their low numbers. Note the rapid decrease among adults on Stellwagen Bank beginning after 1988, and the decrease among juveniles on Stellwagen beginning in 1992. Jeffreys Ledge values were highest in the final three years, after the general decrease on Stellwagen Bank.

Number of whales per day

One of the clearest indicators of habitat use is the number of identified humpback whales sighted on Stellwagen Bank each day. This measure incorporates two of the above components—the number of whales identified as well as how often they were sighted in the area. Throughout the study period, a mean of 12.7 (SD=11.31, n=1,072) whales were identified per day, ranging from an annual high of 17.7 (SD= 15.30, n=153 days) in 1988 to a low of 0.9 (SD=0.76, n=97 days) in 1994 (Fig. 4). Adults and juveniles again showed different trends. Adults per day declined steadily from 14.4 in 1988 to 0.1 in 1994 (B=–2.21, P<0.001), whereas juveniles showed no clear trend, with a high of 8.8 in 1991 and a low of 0.8 in 1994 (B=–0.44, P=0.501). Juvenile values showed a clear peak in 1990–91 as compared with other years (Fig. 4).

Vertical prey density Mean overall vertical prey density decreased from 19.1% with prey traces in 1990 to 2.8% with prey traces in 1992 (B=–0.38, P<0.001) (Table 4). Similar significant decreases were seen in each vertical quarter of the water column (Table 4).

Although it was impossible to determine prey type from traces alone, catches of groundfish (mainly Atlantic cod [*Gadus morhua*] and haddock [*Melanogrammus aeglefinus*]), and bluefish (*Pomatomus saltatrix*) in the immediate area of trace recordings

Table 4

Percentage of the water column with echo-sounder prey traces by year in each quarter. Mean depth was 38.4 meters.

	Quarter of the water column				
Year	Top 25%	2nd 25%	3rd 25%	4th 25%	Total
1990	17.2%	15.0%	16.8%	24.3%	19.1%
1991	3.1%	4.5%	7.3%	12.7%	7.9%
1992	1.4%	0.3%	0.8%	1.1%	2.8%

by party-fishing boats indicated that sand lance were the predominant fish prey in stomach contents of humpback whales; some small mackerel (*Scomber scombrus*) and herring were also observed in stomachs in much lower frequencies. Herring were more prominent in October during each field season, when only a small number of echo-sounder data points were recorded.

Jeffreys Ledge

Total number of humpback whales identified The number of humpback whales we identified on Jeffreys Ledge increased from a low of 35 (in 1988) to a high of 138 (in 1992) (B=19.57, P=0.004; Fig. 2). Although there was a generally increasing trend, there was a sudden increase from 58 in 1991 to 138 in 1992.

The increase among adult whales also showed a significant increase across years (B=17.25, P=0.003). Although juveniles increased steadily throughout the period, and suddenly from 1991 to 1992, they did not do so at a significant rate (B=1.357, P=0.201). (The same analysis without 1992 data, where there were an unusually high number of juveniles, does show a statistically significant increasing trend among juveniles [B=0.914, P=0.006]). Cow-calf pairs also showed a significantly increasing trend (B=1.429, P=0.049).

In each year, identified humpback whales on Jeffreys Ledge were biased toward adults. No more than 17 juveniles were photographed on Jeffreys Ledge in any year, and the number of juveniles photographed exceeded 10 in only a single season (1992). The ratio of adult to juvenile whales ranged from a high of 34.0:1 in 1988 to 7.1:1 in 1992, higher in all cases than the adult:juvenile ratios on Stellwagen Bank.

Number of whales per day The mean number of whales per day ranged from a low of 2.9 (SD=1.9, n=22) in 1989 to a high of 9.2 (SD=7.7, n=138) in 1994 (Fig. 4; B=0.98, P=0.022). In 1993 and 1994, the only years with coverage comparable to Stellwagen Bank levels, means of 6.2 (SD=6.9, n=116) and 9.2 (SD=7.7, n=138) whales were identified on each day of coverage, respectively.

The pattern of humpback abundance on Jeffreys Ledge showed surprising seasonal consistency throughout the study. Sightings were sporadic during May, June, and early July, with few, if any, concentrations of whales observed. In all years, concentrations increased from late July through September, with whales still abundant in three of the seven Octobers observed (1988, 1989, 1993).

Identification comparison To determine whether the whales using Jeffreys Ledge were the same as those previously inhabiting Stellwagen Bank, we examined how many of the 210 humpback whales identified on Jeffreys Ledge in 1992–94 had been previously sighted on Stellwagen Bank. Of this group, 123 (58.5%) were photographed on Stellwagen Bank during 1988–89. When the 17 animals that had not yet been born in 1988–89 were also discounted from the Jeffreys population, 63.7% of all animals were found to have been seen previously on Stellwagen. By comparison, only 35 (16.6%) of the Jeffreys Ledge whales were also seen on Stellwagen Bank during the 1992–93 period, or 16.6% of the total Jeffreys Ledge population.

Discussion

Humpback whales, especially adult and cow-calf pairs, decreased their use of Stellwagen Bank drastically between 1988 and 1994. The decreased use is reflected in decreased numbers of whales identified, decreased numbers of whales (regardless of age class) per day, and decreased adult occurrence and occupancy. The decline led to a virtual abandonment in 1994, when only seven humpback whales were seen on Stellwagen, and only two of those had occupancy periods longer than ten days. The decline in whale use corresponds with a decline in the amount of echo-sounder prey traces at the sites on Stellwagen Bank where whales were found over three years during the study. Although adults showed a clear decreasing trend on Stellwagen Bank, juvenile whales showed a less clear pattern. However, even juveniles showed a rapid decrease in use from 1991 to 1994.

The increase in juvenile whales on Stellwagen Bank during 1990–91 while adult use decreased may also be a more subtle indicator of a shift in habitat quality. Previous work has shown that juvenile humpback whales are often found in areas where prey density is lower than in areas where adults predominate (Weinrich and Kuhlberg, 1991; Belt et al.[5]), and may, therefore, be considered suboptimal

habitat for the species. The vertical distribution of prey has also been reported to be different between concentration areas of the two age classes. Adults are found where prey is concentrated in the upper reaches of the water column (Belt et al.[5]) where a humpback whale's bubble and cooperative feeding strategies are most effective (Hain et al., 1982; D'Vincent et al., 1985; Weinrich et al., 1992; Weinrich et al.[6]) or where foraging is most efficient because energy expenditures associated with diving are lowest (Dolphin, 1987). Juveniles appear to concentrate more often in areas where prey are predominantly subsurface, often feeding on or near the sea floor (Swingle et al., 1993; Hain et al., 1995; Belt et al[5]; Weinrich et al.[6]). In the years where juvenile use increased while adult use decreased (1990–91), echosounder data showed that prey were most concentrated in the bottom 25% of the water column. Even within the year 1990, prey traces were found to be more common in the upper portions of the water column on days when more adult whales than juveniles were present (Belt et al.[5]).

These findings suggest that there are multiple ways of assessing habitat quality for whales. Past reports of population trends have included only the number of whales sighted per unit of effort as a guide to habitat quality (Payne et al., 1986, 1990; Piatt et al., 1989). However, indicators such as independent trends in occurrence and occupancy of individual whales, the number of individuals identified over a given time period, and even the age class of individuals, may also be important indicators of habitat quality. Although all of these measures (except the last) are factors of sightings per unit of effort, these individual components may be illuminating in detailed studies of a particular area. Prey type, for instance, could influence factors such as occurrence or occupancy (or both). In this case, a relatively nonmigratory prey species, such as sand lance (which are tied to areas of particular bottom substrate and topography) could lead to residency extremes (with whales staying in an area for prolonged periods or avoiding the area altogether), while a less habitat-restricted prey (such as herring) could lead to highly variable intraseason distribution patterns.

Although the number of whales on Stellwagen Bank showed a dramatic decrease, the number of whales photographed on Jeffreys Ledge more than doubled in the last three years of the study. The corresponding increase in observer effort during the same period no doubt had some effect on the dramatic increase in both the number of identified individuals and the mean number of whales identified per day. However, existing opportunistic data were collected following the 1992 season because of the increased use of the area suggested from our dedicated vessel surveys, where methods remained standard across years. Further, captains of whale watching boats and naturalists who had worked on Jeffreys Ledge since the mid-1980's unanimously agreed that there was a sudden, dramatic increase in daily whale sightings beginning in 1992. Therefore, we fully believe that an increase in effort is not the sole, or even the primary, cause for any increase in humpback whale numbers reported beginning in 1992.

Our data show that the sudden increase in humpback whale abundance on Jeffreys Ledge was primarily the result of whales seen on Stellwagen Bank earlier in the study relocating for much or all of their summer feeding season. What is perhaps more surprising is the relatively small number of whales that appeared in both areas during 1992 and 1993, despite the relative nearness of these areas to each other. Most of those whales photographed in both areas were seen on Stellwagen Bank for a brief period in October 1993, when herring stocks are known to migrate through the area (Fogarty and Clark[7]).

The consistent timing of whale aggregations on Jeffreys Ledge in each year (starting in early summer) corresponds with both the major influx of herring onto the Ledge and the start of their spawning season (USDC, 1991; Fogarty and Clark[7]). The biomass of the Georges Bank herring population (of which this is a segment—Stephenson and Kornfeld, 1990; Fogarty and Clark[7]) has increased dramatically over the past decade and, by 1991, was comparable to that of its pre-exploitation size (Stephenson and Kornfeld, 1990; Sherman, 1992; NMFS[8]). Echo-sounder data, observation of surface prey, and catches of local fishing boats all indicated that herring were common on Jeffreys Ledge at the same time and location as aggregations of

[5] Belt, C. R., M. T. Weinrich, and M. R. Schilling. 1991. Effects of prey density on humpback whale (*Megaptera novaeangliae*) distribution in the Southern Gulf of Maine. P. 6 *in* Abstracts of the 9th biennial conference on the biology of marine mammals. Society for Marine Mammalogy, Chicago, IL.

[6] Weinrich, M. T., C. R. Belt, M. R. Schilling, and M. E. Cappellino. 1985. Habitat use patterns as a function of age and reproductive status in humpback whales. Abstract *in* Abstracts of the 6th biennial conference on the biology of marine mammals. Society for Marine Mammalogy, Lawrence, KS.

[7] Fogarty, M. J., and S. H. Clark. 1983. Status of herring stocks in the Gulf of Maine region for 1983. Woods Hole Laboratory Reference Document 83-46, NMFS, NOAA, 33 p. [Available from Northeast Fisheries Center, Woods Hole, MA.]

[8] NMFS (National Marine Fisheries Service). 1992. Report of the thirteenth Northeast regional stock assessment workshop (13th SAW). Northeast Fisheries Science Center Document 92-02, Northeast Fisheries Center, NMFS/NOAA, Woods Hole MA. 71 p.

whales. The area is also a primary location for seine fishing for herring off New England. Herring seiners were observed fishing or transiting to or from areas of whale aggregation daily during summers 1992–94.

Although herring stocks were increasing, our data indicated that prey available for whales on Stellwagen showed a marked decrease, corresponding to a decrease in sand lance populations throughout the Northeast ecosystem (Sherman, 1992). This decrease in prey would be expected given the documented inverse relation between sand lance and herring or mackerel stocks, primarily due to direct predation (Fogarty et al., 1991). Although we cannot assign a definitive prey type to our echo-sounder traces from Stellwagen, the documented importance of sand lance as a prey for whales on Stellwagen Bank through observations of prey in the mouths of feeding whales (Hain et al., 1982; Weinrich et al., 1992), the direct observation of sand lance on Stellwagen Bank (Hain et al., 1995), prey in fish stomachs, and the lack of other suitable prey records throughout the years suggest that sand lance remained the predominant prey type for whales in that location.

We propose that humpback whales feeding in the Gulf of Maine ecosystem have shifted from their primary distribution of the mid-1970's through the late-1980's as a result of a shift in the abundance of available prey. Although we have considered only a small portion of the Gulf of Maine habitat, our findings correspond with other data from the same period. In the western side of the Great South Channel (an important area for whales from 1979 to 1991 where sand lance were the primary prey [Kenney and Winn, 1986; Payne et al., 1990]) humpback whale sightings were sporadic after July 1991 (Francis[9]; Clapham[10]; Mattila[11]). Off Mt. Desert Rock, Maine, where humpbacks were virtually absent throughout the 1980's, numbers of whale sightings increased to levels far above those of the mid-1970's (Fernald[12]). Surveys conducted in 1993 on Georges Bank by researchers from the YONAH (Years of the North Atlantic Humpback) project also sighted large numbers of humpbacks, including many animals photographed on Stellwagen Bank in previous years (Clapham[10]).

If a resurgence of herring is responsible for shifts in distribution and in primary prey type, it suggests that the distribution of humpback whales through the late 1970's and 1980's may have been a human-induced consequence. The "explosion" of sand lance in the mid- to late 1970's is thought to be primarily the result of the virtual elimination of herring due to overfishing. If this is true, we hypothesize that our observed distribution of whales from 1992 to 1994 should remain relatively stable over the course of a fairly long period because the current situation would be closer to a "natural" ecosystem.

Alternatively, fluctuations in primary prey may occur naturally, and may take place regardless of human interference. If this is true, we hypothesize that whale distributions will show fluctuations that may be cyclical. New England ground-fishermen have for years talked of regular cycles in sand lance abundance, although there are no scientific data to support this often-made contention.

Regardless of which hypothesis, if either, proves true, our data show a shift in both distribution and primary prey type for humpback whales in southern New England waters in recent years. Because this shift has been so complete, it will be interesting and illustrative to see whether, and how, other potentially prey-dependant humpback whale life history parameters, such as reproductive patterns, social behavior, and demographics of whales, all well-documented during a period of explosive sand lance abundance (Clapham and Mayo, 1990; Weinrich, 1991; Weinrich and Kuhlberg, 1991; Clapham et al., 1992), change in response to these ecosystem alterations.

[9] Francis, L. 1995. Atlantic Cetacean Research Center, PO Box 1413, Gloucester, MA 01930. Personal commun.
[10] Clapham, P. 1995. Smithsonian Institution, Washington, DC. Personal commun.
[11] Mattila, D. 1995. Center for Coastal Studies, PO Box 1036, Provincetown, MA 02657. Personal commun.
[12] Fernald, T. 1995. Allied Whale, College of the Atlantic, Bar Harbor, ME 04609. Personal commun.

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Temporal variation in sexual maturity and gear-specific sex ratio of the vermilion snapper, *Rhomboplites aurorubens*, in the South Atlantic Bight*

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Abstract.—Percentages of mature male and female vermilion snapper, *Rhomboplites aurorubens*, based on total length (TL) and age were calculated for five three-year periods during 1979–93. Males and females collected during 1982–87 became sexually mature at a smaller size and younger age than individuals collected during 1979–81. The median TL at maturity for females decreased from 160 mm in 1979–81 to 151 mm in 1985–87. The median TL at maturity for males was 145 mm during 1979–81. During 1985–87 all males were mature at 140 mm. The temporal shift toward a smaller size at maturity was more pronounced in males than in females. The percentage of mature males at age 1 significantly increased from 63.6% in 1979–81 to 100% in 1985–87 and afterwards. More than twice as many females at age 1 were mature in 1985–87 (48.6%) as in 1979–81. The decline in size and age at maturity may have been caused by fishing pressure that gradually increased during the 1980's.

The sex ratio of vermilion snapper was dependent upon latitude and gear type but was generally independent of water depth, fish length, and sampling years. Although the sex ratios were significantly different among latitudes, there were no trends among latitudes 31°N, 32°N, and 33°N. The percentage of females was 72.1%, 68.0%, and 59.9% for vermilion snapper caught by trap, hook-and-line, and trawl, respectively. Reasons for the difference in sex ratio among gear types are unclear, suggesting that caution must be used when interpreting sex ratios estimated for any fish species collected by various gear types.

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The spawning potential ratio (SPR) has been widely used by U.S. fishery management councils to define overfishing of a fish stock (Goodyear, 1993; Rosenberg et al., 1994; SAFMC[1]). To estimate SPR, life history characteristics (e.g. growth and reproduction) are required and are generally assumed constant among years (Gabriel et al., 1989). However, these parameters, particularly maturity schedules, are not static. They can change in response to fishing pressure, predator and prey abundance, stock composition, and other biotic and abiotic environmental factors (Wootton, 1990). Ignorance of temporal changes in life history parameters may result in the use of incorrect data by fishery managers and therefore may be a reason why fish stocks fail to be protected from overfishing (Rosenberg et al., 1994).

Vermilion snapper, *Rhomboplites aurorubens*, from the South Atlantic Bight (SAB) occur in shelf and upper-slope waters between depths of 26 and 183 m (Grimes, 1978). This species spawns multiple times during a prolonged spawning season (April through September: Grimes and Huntsman, 1980; Cuellar et al., 1996). Vermilion snapper have been of extreme commercial and recreational importance along southeastern states since the early 1980's. Total landings in this region have increased over the years with a peak in 1991 (Zhao and McGovern[2]). However, recent studies have suggested that vermilion snapper are overfished. The stock abundance estimated by virtual population analysis (VPA) has declined since 1984 (Zhao and McGovern[2]). The relative abundance represented by catch per unit of effort (CPUE) markedly declined during 1988–93. There has also been a significant decrease in mean length of vermilion snapper caught by fishery-independent surveys and by the headboat and commercial fishery (Zhao and McGovern[2]). Changes in life history characteristics induced by intense harvesting have been reported for vermilion snapper. Zhao et al. (1997) validated the ageing

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method of otolith sections and demonstrated that size-at-age decreased with time. Collins and Pinckney (1988) reported preliminary evidence that vermilion snapper caught in 1978–80 from SAB became reproductively mature earlier in life than those caught in 1972–74. Grimes and Huntsman (1980) determined that vermilion snapper were gonochorists, females (62.5%) significantly outnumbered males, and the sex ratio was dependent on fish length. However, Nelson (1988) reported that the sex ratio of vermilion snapper from the Gulf of Mexico differed from 1:1 in favor of males (54.5%). He also reported that area and season had a significant effect on this ratio. Although what may have caused the difference in sex ratios of two studies was unknown, limited sample sizes made their comparisons among areas, lengths, or seasons less convincing (Grimes and Huntsman, 1980: n=874; Nelson, 1988: n=881).

In this paper, we investigated the percentage of mature vermilion snapper at each length class and age for each sex and examined the temporal change in maturity schedules during 1979–93. We also determined the sex ratio of vermilion snapper according to depth and latitude of sampling sites, fish length, sampling period, and types of fishing gear used.

Materials and methods

Data were collected from the SAB during 1979–93 by reef fish surveys of the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program. Most vermilion snapper were captured by standardized hook-and-line and trapping gear during the spring and summer of 1979–93 (Collins, 1990; Collins and Sedberry, 1991). In addition, many vermilion snapper were obtained from the MARMAP trawling program that was terminated in 1988. In the field, fish were measured to the nearest mm (TL and FL) and weighed to the nearest gram (whole body weight). Water depth, latitude, and longitude of sampling sites were recorded. The posterior portion of the gonad was removed and preserved in 10% formalin buffered with seawater. In the laboratory, sex and maturity stages were determined by examining the stained gonad sections according to standard MARMAP histological criteria (Cuellar et al., 1996). All gonad samples taken in 1987–93 were examined with histological methods. During 1979–86, sex of specimens was determined and a reproductive condition was assigned in the field by using clearly defined visual staging criteria. The definitions of maturity stages by gross visual inspection were confirmed to be accurate by histological examination during 1978–80 (Collins and Pinckney, 1988). The codes used for defining maturity stages were consistent between histological and macroscopic methods. Seven reproductive stages were used: 1) immature, 2) developing, 3) running ripe, 4) spent, 5) resting, 6) developing with evidence of spawning in the previous week, and 7) mature, but stage-unknown. Mature fish included those in stages 2–7.

Percentages of mature males and females based on total length (TL) and age were calculated for five periods, each corresponding to a three-year interval, i.e. 1979–81, 1982–84, 1985–87, 1988–90, and 1991–93. Because the monthly distribution of samples was not necessarily similar among periods, it was essential to define a standard month(s) if comparison of maturity schedules among years was to be meaningful. In addition, the reproductive condition was most discernible and the sizes and ages at first maturity could be determined during and immediately prior to the spawning season. Therefore, we used the data only from May and June that corresponded to the time of slow somatic growth. Age assignments of vermilion snapper were based on the number of annuli on otolith sections (Zhao et al., 1997). We took into consideration knowledge of the time of annulus formation, the relative growth of the otolith margin, the date of sampling, and used a January 1 hatching date. Because only a part of the samples was aged, some sexed and maturity-determined samples did not have age information.

Although the variation in gear type, latitude, and depth of sampling sites should have been included in the maturity analysis before the data were pooled, limited sample sizes of small (TL<170 mm) and young (age-1) vermilion snapper prevented us from comparing maturity schedules by area (latitude) or by gear type. However, 97% of the males and females smaller than 170 mm were collected by trawl in consistent depth ranges during 1979–90. A majority of these small fish were collected from similar areas, with 88% males and 82% females from latitude 31°N, and 12% males and 18% females from 32°N. Thus, gear selectivity and geographical distribution can be disregarded as sources of bias in comparison of maturity schedules among periods.

As recommended by Trippel and Harvey (1991), the G-test was used to compare maturity schedules of each sex among periods with the same length class or the same age (e.g. age 1). Maturity schedules between sexes at age 1 were compared for the periods of 1979–81 and 1985–87 respectively, when sample sizes of both sexes were sufficient. When conditions of the G-test were not met, Fisher's exact test was used (Zar, 1984). When the percentages of mature fish of each sex in 20 mm TL intervals exhibited a successive increase with length, the median length

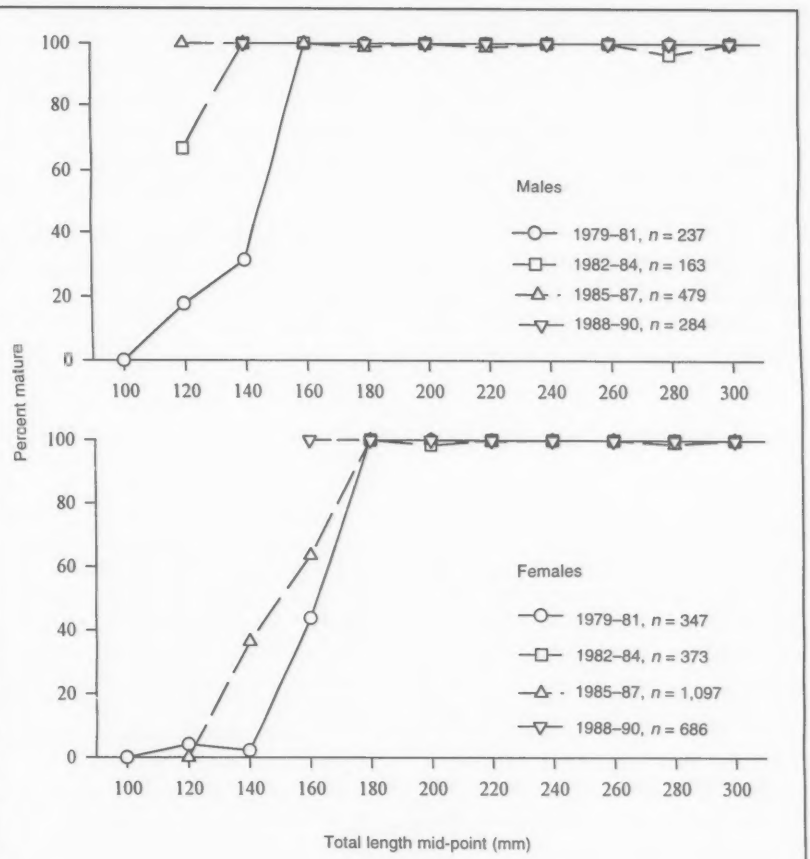

Figure 1

Percentages of mature males and females in each size class of vermilion snapper collected in May and June of 1979–90.

at sexual maturity (TL_{50}) was calculated by probit analysis following the recommendation of Tripple and Harvey (1991). The likelihood ratio test at a significance level of 0.10 was used to determine if the probit model could be fitted to the observations of maturity-at-length (SAS Institute, 1990).

Because sex ratio may change with water depth and latitude of sampling sites, fish length, sampling year, gear, or season (Grimes and Huntsman, 1980; Nelson, 1988), all sexed samples, including mature and immature individuals between 1979 and 1993, were split into the same five periods as described above for maturity analysis. The time frame was increased to May through August to increase the sample size. We compared the percentages of females among varying water depths (midpoints: 25, 35, 45, and 55 m), latitudes (31°N, 32°N, and 33°N), length classes (TL=100 – 450 mm, with 50-mm intervals), periods, and gear types (traps, hook-and-line, and trawl). Latitudes of 31°N, 32°N, and 33°N refer to 31°00'–31°59'N, 32°00'–32°59'N, and 33°00'–33°59'N, respectively. When the independence between sex ratio and one of above factors was tested, other factors were kept consistent. The chi-square test and Fisher's exact test were used to decide the independence. As a reference, Bonferroni's method was used to adjust the significance level, i.e. $\alpha'=0.05/m$, where m = the number of cases (Sokal and Rohlf, 1995). First, we compared the percentage of female vermilion snapper taken from varying depths with the same length classes (TL=200–249 mm and TL=250–299 mm respectively), same latitude (32°N), same periods, and same gear type. Seventy-three percent of the vermilion snapper were collected from latitude 32°N during 1979–93, and eighty percent of them were between 200 and 299 mm TL. If the hypothesis

of independence between sex ratio and depth was not rejected, the data from all depth classes were pooled to compare further the percentage of females among latitudes, other factors (length, period, and gear) being consistent. If the hypothesis was rejected, data from a certain depth class were chosen for further comparison. In a similar fashion, we compared the percentage of females among length classes, periods, and gear types.

The statistical methods available in SAS were used to analyze data of maturity and sex ratio (SAS Institute, 1990). Rejection of the null hypothesis was based on a significance level of 0.05, unless otherwise noted.

Results

Maturity schedules

Males and females collected in 1982–84 and 1985–87 became sexually mature at a smaller size than individuals collected in 1979–81 (Fig. 1). For instance, 31% of male vermilion snapper collected in 1979–81 were mature at 140 mm. However, 100% of males taken at the same size during 1982–90 were mature. All fish taken in May and June of 1991–93 were larger than 180 mm and mature, and therefore were not included in our analysis. There was a significant temporal increase in the percentage of mature males among 1979–81, 1982–84, and 1985–87 at 120 mm (Fisher's exact test: two-tailed $P<0.01$), and at 140 mm (two-tailed $P<0.005$). The percentage of mature females also showed a significant increase with time for 140-mm individuals collected between 1979–81 and 1985–87 (two-tailed $P<0.005$). The observed differences in the percentage of mature females at 160 mm collected during 1979–81, 1985–87, and 1988–90 were not statistically significant (Fig. 1). Males larger than 140 mm and females larger than 160 mm were not tested because all fish were mature.

The likelihood ratio tests indicated that the probit model could be used to describe the maturity at length during 1979–81 for both males (likelihood ratio $\chi^2=2.721$, $P>0.10$) and females (likelihood ratio $\chi^2=1.407$, $P>0.10$), and for females during 1985–87 (likelihood ratio $\chi^2=4.647$, $P>0.10$). The median TL at maturity of males was 145 mm (95% limits: 135–203 mm) during 1979–81. The TL_{50} of females was 160 mm (95% limits: 155–164 mm) in 1979–81 and 151 mm (95% limits: 143–156 mm) in 1985–87.

There was a significant increase in the percentage of mature age-1 males with time between 1979–81, 1982–84, and 1985–87 (Fisher's exact test: two-tailed $P=0.013$) (Table 1). The percentage of mature age-1 females increased ($G=5.318$, $P=0.021$) between 1979–81 and 1985–87. More than twice as many age-1 females were mature in 1985–87 (48.6%) as in 1979–81 (23.1%). The median age at sexual maturity could not be calculated because of the abrupt transition from immature to mature.

Males matured at a smaller size and younger age than females (Fig. 1; Table 1). During 1979–81, TL_{50} for males (145 mm) was smaller than that for females (TL_{50}=160 mm). Although TL_{50} for males in 1985–87 could not be calculated, it was observed that the TL_{50} of males declined with time faster than that of fe-

Table 1

Percentages of sexually mature vermilion snapper caught in May and June of 1979–93. Numbers of fish in each category are given in parentheses. Blanks indicate no data available for that category. There were significant ($P<0.05$) differences in percent mature of age-1 fish among periods for each sex.

Period	Age 1	Age 2	Age 3	Ages 4+
Males				
1979–81	63.6 (11)	100.0 (15)	100.0 (12)	100.0 (13)
1982–84	85.7 (7)			100.0 (28)
1985–87	100.0 (19)	100.0 (12)	100.0 (10)	100.0 (55)
1988–90	100.0 (2)	100.0 (4)	100.0 (4)	100.0 (47)
1991–93			100.0 (1)	100.0 (32)
Females				
1979–81	23.1 (39)	91.3 (23)	100.0 (9)	100.0 (9)
1982–84		100.0 (4)	100.0 (6)	100.0 (67)
1985–87	48.6 (35)	95.8 (24)	100.0 (18)	100.0 (135)
1988–90	100.0 (2)	100.0 (8)	100.0 (10)	100.0 (104)
1991–93			100.0 (3)	100.0 (86)

males (Fig. 1). During 1979–81 and 1985–87, the percentage of mature males at age 1 was significantly larger than that of females at the same age (Table 1; 1979–81: Fisher's exact test, two-tailed P=0.024; 1985–87: G=20.252, P<0.001).

Sex ratios

More vermilion snapper were caught by traps and hook-and-line in the depth range of 40–49 m than in other depth classes (Table 2). The trawl was generally deployed in shallower water (20–39 m) than were traps and hook-and-line. These three gear types were deployed most often in latitude 32°N than in other areas (Table 2). To exclude the effects on sex ratios from varying latitude, fish length, years, and gear types, we used the data collected from the same latitude (32°N), length (200–249 mm or 250–299 mm TL), period, and gear when the independence between sex ratio and depth was tested. Sample sizes in all categories were not always sufficient for a chi-square test. If the expected frequency of a depth-class was unacceptably low, that data was discarded from the contingency table. When sample sizes of depth

Table 2

Numbers of sexed vermilion snapper collected from May through August during 1979–93 by depth and latitude of sampling sites. Blanks indicate that no samples were available for that category.

Period	Depth midpoint (m)	Traps						Hook-and-line				Trawl		
		30°N	31°N	32°N	33°N	34°N	Total	31°N	32°N	33°N	Total	31°N	32°N	Total
1979–81	15												3	3
	25		26				26	27	10		37	5	97	102
	35			1			1	5	10	27	42	242	120	362
	45			8			8		326		326			
	55													
	65													
	Total		26	9			35	32	346	27	405	247	220	467
1982–84	15													
	25			21			21	6	42		48	29	217	236
	35			50			50		31		31		28	28
	45			298			298		214		214			
	55			100			100		27		27			
	65								7		7			
	Total			469			469	6	321		327	19	245	264
1985–87	15		129				129							
	25							13			13	283	22	305
	35								1		1		173	173
	45		20	367			387		145		145			
	55			95			95	17	114		131			
	65													
	Total		149	462			611	30	260		290	283	195	478
1988–90	15													
	25		44	111	80		235	50	53	27	130			
	35	3	13	70			86	22	12		34			
	45			406	23		429		226		226			
	55	2		153			155		118		118			
	65			1			1							
	Total	5	57	741	103		906	72	409	27	508			
1991–93	15			9			9							
	25		155	69	81	10	315	1			1			
	35		104	84	155	6	349		10	4	14			
	45	3		124			127		35		35			
	55	18		286			304		14		14			
	65			4			4							
	Total	21	259	576	236	16	1,108	1	59	4	64			

classes were similar to one another and were small relative to the size of a contingency table, Fisher's exact test was used instead of a chi-square test (Zar, 1984). All tested cases supported the null hypothesis of independence between sex ratio and depth, except for the samples of 200–249 mm TL fish caught with traps during 1982–84 (Table 3). After allowance for multiple-testing (α'=0.05/18=0.0028), none of the cases was statistically significant.

Since there were no significant differences among depth classes, we pooled the data from all depth classes to compare the percentage of females among

Table 3

Comparison of percentages of females among water depth-classes with the same latitude (32°00'–32°59' N), length ranges (TL=200–249 mm and 250-299 mm), period, and gear type. % = female percent. n = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of depth. Blanks indicate no or few samples available for comparison. df = degrees of freedom.

		Traps				Hook-and-line				Trawl			
	Depth midpoint	TL=200–249		TL=250–299		TL=200–249		TL=250–299		TL=150–199		TL=200–249	
Period	(m)	%	n	%	n	%	n	%	n	%	n	%	n
1979–81	25									54.6	55	53.9	39
	35									66.7	48	59.7	62
	chi-square									1.572		0.333	
	P									0.210		0.564	
	df									1		1	
	Reject H_0									No		No	
1982–84	25	83.3	18	100.0	2[1]	66.7	15	57.7	26			58.9	112
	35	91.7	36	84.6	13	64.7	17	80.0	10			65.2	23
	45	67.1	152	69.1	97	74.4	43	71.6	109				
	55	80.0	45	75.6	41	75.0	8	40.0	15				
	chi-square	11.28		1.708		Fisher's[2]		Fisher's[2]				0.314	
	P	0.010		0.426		0.859		0.056				0.575	
	df	3		2								1	
	Reject H_0	Yes		No		No		No				No	
1985–87	25											57.9	19
	35											62.2	135
	45	86.9	206	72.4	134	68.6	51	63.9	72				
	55	76.7	60	82.4	34	61.4	44	71.2	59				
	chi-square	3.727		1.414		0.550		0.783				0.132	
	P	0.054		0.234		0.458		0.376				0.716	
	df	1		1		1		1				1	
	Reject H_0	No		No		No		No				No	
1988–90	25	82.7	81	73.7	19	61.8	34						
	35	77.1	48	79.0	19								
	45	72.5	189	67.1	176	65.1	126	60.0	45				
	55	64.9	74	75.0	76	70.0	60	71.8	39				
	chi-square	6.808		2.484		0.745		1.286					
	P	0.078		0.478		0.689		0.257					
	df	3		3		2		1					
	Reject H_0	No		No		No		No					
1991–93	25	80.0	30	84.6	13[1]								
	35	74.5	47	80	20								
	45	70.0	30	77.9	68								
	55	64.4	160	73.5	102								
	chi-square	3.910		0.649									
	P	0.271		0.723									
	df	3		2									
	Reject H_0	No		No									

[1] The row was discarded from the contingency table because of its excessively low expected frequency.
[2] When conditions for a chi-square test were not met, Fisher's exact test was used.

latitudes with other factors (length, period, and gear) remaining consistent. Six of the 14 tested cases indicated that sex ratio was dependent on latitude (Table 4). Even after allowance for multiple-testing (α'=0.05/14=0.0036), there were still two cases indicating significant difference (1979–81, trawl, 150–199 TL and 1988–90, traps, 200–249 TL). Because the latitudinal distribution of samples was not similar among periods for any gear type (Table 2), we used only data from the latitude of 32°N in subsequent analyses.

There were no significant differences in percentage of females caught by traps among length classes 200–249, 250–299, and 300–349 mm during 1982–84, 1988–90, or 1991–93 (Table 5). During 1979–81, the hypothesis of independence between sex ratio and length was rejected for fish caught by hook-and-line within the length range of 150–449 mm. However, it was not rejected within 200–299 mm (Table 5). Thus, the common TL range of vermilion snapper caught by hook-and-line was 200–299 mm, within which the sex ratio was independent of length during 1979–93. There were no significant differences in percentages of females caught by trawl within 150–249 mm during 1979–81 and 1985–87 (Table 5). After allowance for multiple-testing (α'=0.05/12=0.004), none of the 12 cases showed significant difference.

We compared the percentage of females among periods by pooling data for each gear type within the common TL range and periods when the sex ratio was independent of length. There were no signifi-

Table 4

Comparison of percentages of females among latitudes with the same length ranges (TL=200–249 mm and TL=250–299 mm), period, and gear type. All data were pooled from various water depth classes. % = female percent. n = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of latitude. Blanks indicate no or few samples available for comparison.

		Traps				Hook-and-line				Trawl			
	Latitude	TL=200–249		TL=250–299		TL=200–249		TL=250–299		TL=150–199		TL=200–249	
Period	(°N)	%	n	%	n	%	n	%	n	%	n	%	n
1979–81	31					57.1	14	87.5	8	36.5	115	57.1	14
	32					73.6	106	67.6	105	60.2	103	57.4	101
	33					87.5	16	50.0	4				
	chi-square					Fisher's[2]		Fisher's[2]		12.205		0	
	P					0.178		0.352		<0.001		0.984	
	df									1		1	
	Reject H_0					No		No		Yes		No	
1985–87	31	82.6	115	50.0	20	72.7	11	93.3	15	39.4	221	52.3	44
	32	84.6	266	74.4	168	65.6	96	67.2	131	58.3	36	61.7	154
	chi-square	0.234		5.258		Fisher's[2]		Fisher's[2]		4.571		1.260	
	P	0.629		0.022		0.747		0.039		0.033		0.262	
	df	1		1						1		1	
	Reject H_0	No		Yes		No		Yes		Yes		No	
1988–90	31	63.9	36	100.0	4[1]								
	32	73.7	392	70.5	291								
	33	91.8	61	76.7	30								
	chi-square	11.96		0.511									
	P	0.003		0.475									
	df	2		1									
	Reject H_0	Yes		No									
1991–93	31	80.0	235	57.1	7								
	32	68.8	276	76.8	207								
	33	77.7	206	60.0	20								
	chi-square	9.509		3.925									
	P	0.009		0.141									
	df	2		2									
	Reject H_0	Yes		No									

[1] The row was discarded from the contingency table because of its excessively low expected frequency.
[2] When conditions for a chi-square test were not met, Fisher's exact test was used.

Table 5

Comparison of percentages of females among length classes with the same latitude (32°00'–32°59' N), period, and gear type. All data were pooled from various depth classes. % = female percent. n = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of length. Blanks indicate no or few samples were available for comparison.

		Traps			Hook–and–line			Trawl		
Period	TL (mm)	%	n		%	n		%	n	
1979–81	90–149						$\chi^2 = 14.079$	78.6	14	$\chi^2 = 2.293$
	150–199				38.9	18	$P = 0.015$	60.2	103	$P = 0.318$
	200–249				73.6	106	df = 5	57.4	101	df = 2
	250–299				67.6	105		100.0	2[1]	
	300–349				54.6	77				
	350–399				72.4	29				
	>399				54.6	11				
	Reject H_0						Yes			No
1982–84	150–199	66.7	3[1]	$\chi^2 = 1.597$	80.0	5[1]	$\chi^2 = 0.449$	41.0	100	$\chi^2 = 8.847$
	200–249	74.1	251	$P = 0.450$	71.1	83	$P = 0.930$	60.0	135	$P = 0.012$
	250–299	72.6	153	df = 2	67.1	161	df = 3	40.0	10	df = 2
	300–349	65.3	49		67.3	52				
	350–399	80.0	10[1]		66.7	18				
	>399	100.0	3[1]		100.0	2[1]				
	Reject H_0			No			No			Yes
1985–87	90–149	100.0	1[1]	$\chi^2 = 6.844$	0	1[1]	$\chi^2 = 0.515$	66.7	3[1]	$\chi^2 = 0.138$
	150–199	100.0	5[1]	$P = 0.033$	75.0	4[1]	$P = 0.773$	58.3	36	$P = 0.710$
	200–249	84.6	266	df = 2	65.6	96	df = 2	61.7	154	df = 1
	250–299	74.4	168		67.2	131		100.0	2[1]	
	300–349	81.0	21		73.1	26				
	350–399	100	1[1]		100.0	2[1]				
	>399									
	Reject H_0			Yes			No			No
1988–90	90–149			$\chi^2 = 1.048$	33.3	3[1]	$\chi^2 = 1.547$			
	150–199	100.0	5[1]	$P = 0.592$	59.7	62	$P = 0.461$			
	200–249	73.7	392	df = 2	67.1	228	df = 2			
	250–299	70.5	291		68.8	93				
	300–349	75.0	44		41.2	17[1]				
	350–399	57.1	7[1]		25.0	4[1]				
	>399	50.0	2[1]		100.0	2[1]				
	Reject H_0			No			No			
1991–93	150–199	50.0	4[1]	$\chi^2 = 6.035$	100	2[1]	Fisher's[2]			
	200–249	68.8	276	$P = 0.110$	64.5	31	$P = 1.0$			
	250–299	76.8	207	df = 3	64.3	14				
	300–349	63.4	71		25.0	4[1]				
	350–399	71.4	14		60.0	5[1]				
	>399	50.0	4[1]		100.0	3[1]				
	Reject H_0			No			No			

[1] The row was discarded from the contingency table because of its excessively low expected frequency.
[2] When conditions for a chi–square test were not met, Fisher's exact test was used.

cant differences in percentages of females among periods for either gear type (Table 6). The overall chi-square test indicated a significant lack of independence between sex ratio and gear type (Table 7A). We subdivided the data into 2×2 contingency tables formed by any two gear types. Significant differences in the percentage of females were found between trawl and traps (χ^2=22.642, P<0.001), between trawl and hook-and-line (χ^2=8.424, P=0.004), and between traps and hook-and-line (χ^2=5.166, P=0.023). Therefore, we concluded that traps caught more females than did the other two gear types, and hook-and-line caught more females than trawl. This conclusion was supported by additional analysis with various length

Table 6

Comparison of percentages of females among periods with the same latitude (32°00'–32°59' N) and gear type. All data were pooled from various depth classes. % = female percent. n = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of period. Blanks indicate few samples available for comparison or the null hypothesis of independence between sex ratio and length was rejected in Table 5. df = degrees of freedom.

	Traps (TL=200–349)		Hook-and-line (TL=200–299)		Trawl (TL=150–249)	
Period	%	n	%	n	%	n
1979–81			70.6	211	58.8	204
1982–84	72.6	453	68.4	244		
1985–87			66.5	227	61.1	190
1988–90	72.5	727	67.6	321		
1991–93	71.1	554	64.4	45		
chi-square	0.382		1.199		0.204	
P	0.826		0.878		0.652	
df	2		4		1	
Reject H_0	No		No		No	

Table 7

Comparison of percentages of females among gear types with the same latitude (32°00'–32°59' N). All data were pooled from various depth classes. % = female percent. n = the total number of male and female fish. The null hypothesis (H_0) = sex ratio is independent of gear type. Data were pooled from periods that were used in Table 6. Data with different length ranges were used in A, B, and C. (A) TL ranges were the same as used in Table 6 for each gear; (B) TL = 200–249 mm for all gear types; (C) TL = 186–540 mm, mean TL = 254 mm for traps, TL = 142–560 mm, mean TL = 261 mm for hook-and-line, and TL = 112–256 mm, mean TL = 203 mm for trawl.

	A		B		C	
Gear	%	n	%	n	%	n
Traps	72.1	1734	72.4	919	72.1	1786
Hook-and-line	68.0	1048	68.6	544	66.2	1395
Trawl	59.9	394	60.0	255	61.0	415
chi-square	23.460		14.558		24.938	
P	<0.001		0.001		<0.001	
df	2		2		2	
Reject H_0	Yes		Yes		Yes	

ranges (Table 7B: a single TL range for all gear types; Table 7C: all data available were used with full TL ranges). Vermilion snapper caught by all gear types had an unequal sex ratio that was female-biased (traps and hook-and-line: $P << 0.001$, trawl: $P<0.005$).

Discussion

Maturity schedules

Although data used for maturity analysis were limited to those collected in the same season (May and June) of each period, growth may occur, and stages of maturity may change, within two months. An immature fish in May may become mature in June. If more fish were collected in June of recent years than in 1979–81, the percent mature at a certain age would be overestimated for recent years. The monthly distribution of observations, however, was similar among periods with more than 80% of the fish smaller than 170 mm being collected in May. Relative differences in maturity schedules among periods remained valid throughout the study.

The essential underlying assumption of the maturity analysis is that length, age, and reproduction conditions are correctly measured or determined. In 1985, 1986, 1987, and 1988, only fork lengths (FL) were measured. These FL were converted to TL with TL (mm) = $1.115FL - 0.254$ (Zhao et al., 1997). For other years, observed TL was available. Because the method for ageing vermilion snapper by means of otolith sections has been validated by Zhao et al. (1997) and because the persons who read otoliths in Zhao et al.'s study also read otoliths in our study, incorrect ageing of vermilion snapper is not considered a source of bias. During 1979–86, gonads were examined macroscopically by experienced biologists by means of clearly defined gross morphological staging criteria. These criteria were confirmed to be accurate by histological examination during 1978–80. All gonads, since 1987, were examined by using reliable histological techniques (Cuellar et al., 1996). Therefore, it is believed that sex and maturation were correctly determined. In general, sex and maturity stages can be more reliably determined during the spawning season than in off-seasons. Data used for maturity analysis were only from May and June, the first part of the spawning season, during which errors in maturity determination were not expected. Furthermore, in the present study, all maturity stages of mature fish were pooled in only one maturity state, i.e. mature. As long as immature and mature fish could be distinguished, inaccurate classification of mature substage would not introduce a bias in estimates of age and size at maturity.

This study indicated that both age and length at sexual maturity of vermilion snapper declined over time. This decline may have resulted from increased fishing pressure, because the total landings consis-

tently increased during the 1980's (Zhao and McGovern[2]). The demonstration that the harvest of a fish stock can lead to declines in length or age at maturity has been reported for many fishes, including northeast Arctic cod (Jørgensen, 1990), Pacific salmon (Ricker, 1981), and California halibut (Love and Brooks, 1990). Changes in size or age at maturity may be the result of a density-dependent response to decreased stock abundance, selective removal and incomplete replacement of later-maturing fish by the fishery, or genetic change within a population (Nelson and Soulé, 1987). Jørgensen (1990) attributed a decline in median age-at-maturity in northeast Arctic cod to an increase in length-at-age (i.e. faster growth) coincident with declining stock density, an idea that implicitly assumes a minimum threshold for size-at-maturity. If the scenario of Jørgensen (1990) is correct, declines in length and age should not occur concurrently. Furthermore, Zhao et al. (1997) indicated that the size-at-age of vermilion snapper has decreased with time. Therefore, changes in maturity schedules of vermilion snapper are not part of a density-dependent compensatory response to harvesting, but quite likely a result of the selective removal and incomplete replacement of faster-growing, later-maturing fish by the fishery. If intensive fishing pressure continues, and the early-maturing trait is heritable, length and age at maturity in the population will decrease with time. Life history theory predicts that genetic changes in life history characteristics will occur following increased mortality (Roff, 1992). Harvesting can reverse the relative fitness of genotypes, because an inferior genotype (e.g. slow-growing and early-maturing) in an unexploited population may be more fit under increased fishing pressure (Bergh and Getz, 1989). Early-maturing genotypes reproduce before being fully recruited to the fishery, whereas genotypes that mature at larger sizes or older ages tend to be removed before reproduction. This process would explain the decreasing abundance of larger, immature fish with time and would account for declines in both size and age at maturity. The long-term impacts of size-selective fish harvests may have caused the decline in size-at-age of vermilion snapper through disproportionate harvesting of fast-growing individuals (Zhao et al., 1997). Similarly, it may be that late-maturing genotypes were removed from the vermilion snapper population in the 1980's when fishing pressure was intensive.

Maturity schedules of vermilion snapper collected during 1972–74, prior to heavy exploitation, were investigated by Grimes and Huntsman (1980). They used a gonadosomatic index and indicated that "most fish attain sexual maturity during their third or fourth years of life (186–256 and 256–324 mm TL), but a few precocious individuals may mature in their second year (100–186 mm TL) at about 150 mm TL." It is not rigorous to compare the percent mature, based on age, between Grimes and Huntsman (1990) and the present study because an obvious discrepancy in size-at-age exists between Grimes (1978) and Zhao et al. (1997). It is meaningful, however, to compare maturity schedules based on length between these two studies. The maximum-likelihood estimates from the probit analysis of data from the present study predicted that 50% of males and 15% of females matured by 150 mm during 1979–81 and that 50% females at 150 mm matured during 1985–87. All males and females at 180 mm were mature in the present study. Differences between previous (Grimes and Huntsman, 1980) and present results could be partially due to differences in methods used to determine maturity (Collins and Pinckney, 1988) or may truly reflect the changes in maturity that occurred in the 1970's. The increase in percentage of mature females at 150 mm was faster during the 1980's than during the 1970's (i.e. an increase of 35% in six years from 1979–81 to 1985–87, versus an increase of less than 15% in seven years from 1972–74 to 1979–81). The degree of exploitation may account for the differing rates of change in maturity while the fishery for vermilion snapper was initiated in the 1970's, but heavy exploitation did not occur until the 1980's.

Sex ratios

The chi-square analysis did not suggest significant differences in percentages of females among months (May–August) for any gear type. This information supported the notion that pooling data between May through August would not bias the comparison of sex ratios. Seasonal comparisons of sex ratios could not be done because little sampling was done in fall or winter.

This study showed that the sex ratio of vermilion snapper was dependent on area (latitude) and gear type, but independent of depth of sampling sites, fish length, or sampling years. The reason for the significant differences among latitudes is unknown. However, only 2 of the 14 cases showed a significant difference according to Bonferroni's method (Table 4), and no trend was observed between latitudes. In addition, relatively small sample sizes collected from latitudes other than 32°N may have induced errors in comparison. Therefore, we attribute the difference in sex ratio between latitudes to chance.

Although significantly different, the percentages of females of vermilion snapper collected by traps

and hook-and-line were similar to each other (traps: 72.1%; hook-and-line: 68.0%) but differed from that for trawl capture (59.9%). Trawls caught smaller fish from shallower waters when compared with traps and hook-and-line (Tables 2 and 7C). However, present results indicated that sex ratios were not affected by water depth or fish length. With traps and hook-and-line gear, baits were used to attract fish. If female vermilion snapper were more aggressive in pursuing bait than males, the percentage of females in the catch of traps and hook-and-line could be higher than that in the population. In contrast, no baits were used for trawling, and therefore males and females might be caught with the same probability. If the difference in feeding behavior between sexes can account for the difference in sex ratio between gear, then the sex ratio of vermilion snapper in the population may be correctly represented by the trawl catch. Watanuki et al. (1993) reported that basket traps caught the greatest ratio of female cuttlefish among three types of gear (basket traps, jigs, and trammel nets). More females may be attracted to traps for spawning, but Watanuki et al. indicated that there are probably other unknown factors governing the entry of cuttlefish into traps. Because information on spawning behavior of vermilion snapper is unavailable, we cannot evaluate how the spawning activity of vermilion snapper may affect its vulnerability to different gear types.

We pooled data from all gear types and calculated the overall sex ratio by period. The percentage of females gradually increased from 62% in 1979–81 to 70% in 1991–93. The temporal increase in the percentage of females proved to be an artifact of unequal distribution of catch by gear among periods. Reasons for the difference in sex ratios among gear types are unknown. Caution must be used when evaluating the sex ratios of any fish species collected by various gear types.

Our conclusion of independence between sex ratios and lengths differs from previous studies. Grimes and Huntsman (1980) concluded that the sex ratio of vermilion snapper was dependent on fish length, with the percentage of females increasing in larger size classes. However, the percentage of females within the range of 551–600 mm TL (89.3%, n=32) was obviously higher than those for other length ranges. Thus, it is suspected that the significant chi-square calculated by Grimes and Huntsman (1980) was probably due to this length range. We used the original data published in Table 4 of Grimes and Huntsman (1980) but excluded the data with length greater than 550 mm TL (n=32). We found that sex ratio was independent of length (χ^2=13.105, P=0.108, n=841, df=8, TL=101–550 mm) and thus was in agreement with the conclusion of the present study. A further 2×2 contingency table analysis formed by the TL range of 551–600 mm versus all other length ranges rejected the null hypothesis of independence between sex ratio and length (χ^2=11.732, P=0.001, n=873, df=1). Thus, we confirmed that the sex ratio within 551–600 mm TL is significantly different from those of other length ranges. Because our data had relatively few vermilion snapper larger than 450 mm TL, the conclusion of independence between sex ratio and length may be limited to 450 mm TL or less. However, the similar size-at-age and the same longevity of male and female vermilion snapper do not suggest the percentage of females would increase with length even beyond 450 mm TL (Zhao et al., 1997).

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A polyphasic growth function for the endangered Kemp's ridley sea turtle, *Lepidochelys kempii*

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The Kemp's ridley, *Lepidochelys kempii*, is the smallest of the seven extant species of sea turtle (Marquez, 1994) and is endemic to the Gulf of Mexico and Atlantic coast of the United States (Pritchard, 1989). It has been subject to extensive human exploitation and is the most endangered sea turtle species in the world (Marquez, 1994). Seasonal trawl and pound-net fisheries are major hazards, posing a serious risk to the long-term population viability of the Kemp's ridley (Epperly et al., 1995; Caillouet et al., 1996). Although the Kemp's ridley sea turtle is endangered, the somatic growth and population dynamics of this species are not well known (Chaloupka and Musick, 1997) despite several important growth studies that have been carried out for captive or head-started stocks (Caillouet et al., 1986; Caillouet et al., 1995b). We propose a new growth model for the endangered Kemp's ridley sea turtle that is based on a skeletochronological data set derived recently by Zug et al. (1997) from wild stock sea turtles stranded along the Atlantic Bight and Gulf coasts of the United States. The growth model presented provides a basis for improving our understanding of sea turtle growth dynamics in general and for modeling Kemp's ridley population viability.

Materials and methods

Data set

The data set used here comprised 70 size-at-age records for Kemp's ridley sea turtles—69 records from stranded turtles plus the inclusion of known mean hatchling size (see Marquez, 1994). The data set (n=70) also comprised growth records spanning the postnatal development phase (from 4 to 72 cm straight carapace length, SCL) and including the mature adult phase, but the records were not distributed evenly over this size range. The age estimates were derived from a skeletochronological analysis of wild Kemp's ridley sea turtles stranded along the Atlantic coast of the United States and in the Gulf of Mexico (see Zug et al., 1997). Straight carapace length (SCL) was measured to 0.1 cm and age to 0.1 yr. The original sample of stranded turtles comprised 73 individuals, but age estimates for 4 individuals were not possible because of either 1) a lack of discernible growth rings or 2) uninterpretable irregular growth. Records for these 4 individuals were discarded, yielding the 69 individual turtles used in this study.

The data set also included stranding location, with 79% of the sample comprising turtles stranded on the Atlantic coast. Sex was recorded for 37% of the strandings; no proportional difference was evident between the Atlantic and Gulf of Mexico subsamples. Further details of the strandings data set and the skeletochronological methods used for age estimation can be found in Zug et al. (1997).

The limitations of skeletochronological ageing techniques and the need for caution in interpreting such age estimates for sea turtles have been well discussed elsewhere (Zug et al., 1986; Zug, 1990; Zug et al., 1997). Chaloupka and Musick (1997) have also provided a critical review of sea turtle skeletochronological studies and have discussed the limitations of such studies in terms of age validation, length back-calculation, growth estimation, layer loss adjustment protocols, and implications of the specific time-dependent sampling design implicit in the data set. For instance, the implicit sampling design in the current study was mixed cross-sectional because only the terminal age-size estimate was available for each of the 69 stranded turtles. This sampling design confounds age and cohort effects and thus only an expected or mean growth function can be estimated (see Chaloupka and Musick, 1997).

Statistical modeling approach

The functional relation between size (cm SCL) and estimated age for the 70 Kemp's ridley sea turtles was modeled with a two-stage approach: 1) exploratory data visualization including nonparametric smoothing (see Cleveland, 1993) to

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evaluate the implicit functional form of the growth model without having to specify an explicit and perhaps invalid nonlinear function; and 2) a polyphasic parametric growth function fitted to the size-at-age data on the basis of the functional form implied by the nonparametric smooth. Polyphasic growth means that there is more than one growth phase or cycle in postnatal development, suggesting ontogenetic shifts in growth rates manifested by at least two growth spurts between birth and the onset of adult maturity (see Gasser et al., 1984). The polyphasic growth function used in our study was the Peil and Helwin (1981) parameterization comprising a summation of logistic functions as follows:

$$y_t = \sum_{i=1}^{j} \left\{ \alpha_i \left[1 + \tanh\left(\beta_i (t - \delta_i)\right) \right] \right\} + \varepsilon_{ti} \qquad (1)$$

where y_t = mean length at age t;
α_i = (asymptotic mean)/j length in phase i;
β_i = growth coefficient in phase i;
δ_i = age at the inflection point of phase i;
$\tanh(z)$ = $(e^z - e^{-z})/(e^z + e^{-z})$ and $z = (\beta_i(t - \delta_i))$;
j = number of growth phases; and
ε_{ti} = an appropriate random error structure.

Parameters of the standard logistic function (monophasic with skewed symmetric inflexion and suggesting one growth spurt) are well known to have excellent statistical properties (Ratkowsky, 1990). It was assumed that the polyphasic form (Eq. 1) used here also has sound statistical properties. In principle, Equation 1 was fitted by heteroscedasticity-robust nonlinear least-squares (HRNLS) with a heteroscedasticity-consistent covariance matrix estimator (HCCME) to account for growth variability and measurement error (see Davidson and MacKinnon, 1993). In practice, Equation 1 was fitted with RATS (Doan, 1992), which implements HRNLS with White's HCCME. Otherwise, the generalized method of moments (GMM) approach can be used for robust nonlinear regression estimation (Davidson and MacKinnon, 1993). The age-specific growth-rate function for the Kemp's ridley sea turtle was derived analytically by taking the first derivative of the fitted Equation 1 with the software program MATHEMATICA (Wolfram Research, 1993).

Results

The size and estimated age data for the 70 Kemp's ridley sea turtles presented in Zug et al. (in press) are shown in Figure 1A with a locally weighted regression smoothing known as LOWESS (see Cleveland, 1993) superimposed to reveal the implicit functional form. The LOWESS procedure can be implemented by using S software (Becker et al., 1988). The nonparametric smooth (Fig. 1A) implies a polyphasic function with two sequential growth phases, with the first decelerating around 30 cm SCL and the second

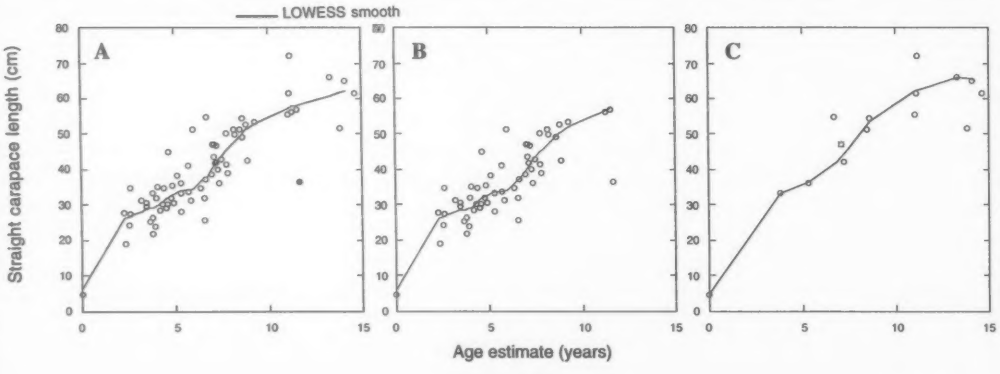

Figure 1

(**A**) Scatterplot of size-at-age estimates for the 69 Kemp's ridley sea turtles stranded along the Atlantic Bight and Gulf coasts of the United States, with an additional estimate of mean hatchling size (age=0 yr). Open circles and solid dot are the original data estimates (n=70) from Zug et al. (1997). Solid dot is the outlier discounted in the parametric model (Table 1). The curve in (A) is a LOWESS (locally weighted robust regression) smooth superimposed to highlight the underlying size-at-age function without presuming the functional form. (**B**) Scatterplot of the Atlantic Bight subsample estimates (n=55), with hatchling size included and a LOWESS smooth superimposed. (**C**) Scatterplot of the Gulf of Mexico subsample estimates (n=14), with hatchling size included and a LOWESS smooth superimposed.

at ≥60 cm SCL. It is proposed that a polyphasic growth model might be a better mathematical description of growth than the monophasic (monotonic) von Bertalanffy (Caillouet et al., 1995b; Schmid, 1995; Zug et al., 1997) or the monophasic (non-monotonic) Gompertz functions (Caillouet et al., 1986) proposed for this species. A similar polyphasic growth function comprising two phases is also evident for the Atlantic Bight subsample (Fig. 1B) and is suggested for the Gulf subsample (Fig. 1C) despite a very sparse data field in the latter case.

Figure 1 also highlights the considerable variability (heterogeneity) inherent in sea turtle growth and why heteroscedasticity-robust estimation procedures (e.g. HCCME, GMM) should be used to derive regression parameter estimates for growth model fits. There is also a major outlier in Figure 1A indicated by a solid dot—this value was discounted in the explicit parametric model fit because no parametric model could be as robust in respect to this outlier as the nonparametric smooth displayed in Figure 1A. Growth variability in sea turtle studies is a complex function of demographic (sex, maturity status) and geographic factors as well as a function of the time-dependent nature of the implicit sampling design (confounding year and cohorts effects) and instrumental measurement error. For instance, Caillouet et al. (1986) have shown conclusive evidence of somatic growth variability due to cohort (year-class) effects for captive reared Kemp's ridley sea turtles. The small sample size, mixed cross-sectional sampling design, and insufficient data on demographic and geographic covariates precluded any reliable estimate of these additional sources of growth record variability in the current study.

The parametric growth curve proposed here to match the nonparametric smooth (Fig. 1A) for the Kemp's ridley data comprises separate logistic growth functions for each of the two inferred growth phases integrated into a single explicit polyphasic function—Equation 1. The statistical fit of this function to the growth data (Fig. 1A) is shown in Table 1. The growth model with robust estimation and with elimination of the extreme outlier (see Fig. 1A) fitted the data well with significant parameter estimates even allowing for family-wise error-rate adjustment, small parameter estimate standard errors, and no aberrant residual behavior (see Judge et al., 1985, or Ratkowsky, 1990, for a discussion of nonlinear regression fitting and goodness-of-fit criteria). Despite the good fit, significant growth variability, probably due to instrumental measurement error and confounding of year and cohort sampling effects, was not accounted for by the model (residual variance: σ^2=29.1).

Table 1

Parameter estimates for the polyphasic logistic growth function (Eq. 1) fitted to the Kemp's ridley sea turtle size-at-age growth data in Zug et al. (1997). See Equation 1 for definitions of parameters.

Parameter	Estimate	Asymptotic standard error	*t*-ratio	Inference
α_1	13.6467	2.7463	4.97	$P < 0.001$
β_1	0.7901	0.2989	2.64	$P < 0.008$
δ_1	1.1169	0.4303	2.59	$P < 0.009$
α_2	17.6595	3.9288	4.49	$P < 0.001$
β_2	0.3059	0.1274	2.40	$P < 0.016$
δ_2	7.6361	0.5407	14.12	$P < 0.001$

The expected polyphasic size-at-age function is shown in Figure 2A (age=skeletochronological age estimate) and presented numerically in Table 2 for comparative purposes. The explicit size-at-age growth function (Fig. 2A) was then differentiated with respect to estimated age by an analytical solution to Equation 1 to derive the age-specific growth rate function (Fig. 2B). The expected age-specific growth rate function (Fig. 2B) displays an initial posthatchling growth rate >5 cm SCL/year, increasing to 11 cm SCL/year ≥1 year of age (Δ_1) or 13 cm SCL, slowing to 2 cm SCL/year by 3–4 years of age (ca. 27 cm SCL), marking the end of the first growth phase (i.e. $2\alpha_1$=27.3 in Table 1; mid-curve asymptote in Figs. 1A and 2A). The growth rate then rises to 6 cm SCL/year near 8 years of age (δ_2) or to 46 cm SCL before declining slowly to negligible growth approaching adulthood ≥15 years of age at a size ≥62 cm SCL, marking the end of the second growth phase (i.e. $2(\alpha_1+\alpha_2)$=62.6 in Table 1; upper asymptote in Figs. 1A and 2A).

Discussion

Monophasic von Bertalanffy growth functions have been proposed for the Kemp's ridley sea turtle by Caillouet et al. (1995b), Schmid (1995), Zug et al., (1997), and others (Marquez, 1994, and references therein). With the von Bertalanffy growth function, however, a monotonic decreasing growth-rate function is implied and hence no growth spurt at any age or size. The statistical validity of that function fitted to a limited data span and of the Fabens mark-recapture analogue used by Schmid (1995) and Zug et al. (1997) has been reviewed critically by Chaloupka and Musick (1997). It is questionable whether a monophasic von Bertalanffy function fits the mean growth profile for the complete postnatal

Table 2

Comparison of size-at-age growth functions for three Kemp's ridley sea turtle growth models. Age = known age for the Caillouet et al. (1995b) model, whereas age = skeletochronological age estimate for the Zug et al. (1997) model and the polyphasic model presented here. SCL = straight carapace length.

	Size-at-age estimate (cm SCL)				Size-at-age estimate (cm SCL)		
Age (years)	Caillouet et al. (1995b)	Zug et al. (1997)	This study (Fig. 2A)	Age (years)	Caillouet et al. (1995b)	Zug et al. (1997)	This study (Fig. 2A)
0 (hatchling)	2.79	8.86	4.32	13	61.30	59.49	61.33
1	18.95	14.85	12.99	14	61.57	61.63	61.91
2	30.72	20.39	22.96	15	61.76	63.62	62.23
3	39.29	25.50	27.93	16	61.90	65.45	62.40
4	45.53	30.23	30.46	17	62.00	67.14	62.50
5	50.08	34.60	33.11	18	62.07	68.70	62.55
6	53.39	38.63	36.77	19	62.13	70.15	62.58
7	55.80	42.36	41.56	20	62.17	71.48	62.59
8	57.56	45.81	46.91	21	62.19	72.72	62.60
9	58.84	48.99	51.92	22	62.21	73.86	62.61
10	59.77	51.94	55.88	23	62.23	74.91	62.61
11	60.45	54.65	58.61	24	62.24	75.89	62.61
12	60.94	57.17	60.32	25	62.25	76.79	62.61

development phase of any sea turtle species (see Chaloupka and Limpus, 1997; Chaloupka and Musick, 1997).

On the other hand, the monophasic form of the Gompertz growth function used by Caillouet et al., (1986) in a single cohort growth study (weight gain) of 10 Kemp's ridley sea turtles held in captivity clearly fitted the data well at least for the observed range (ca. 2–7 years old). In the Gompertz function, a nonmonotonic growth-rate function is assumed with a growth spurt in early development similar to the first growth spurt in our study (see Fig. 2B). Whether growth in Caillouet et al.'s (1986) study might have been better fitted by using a polyphasic

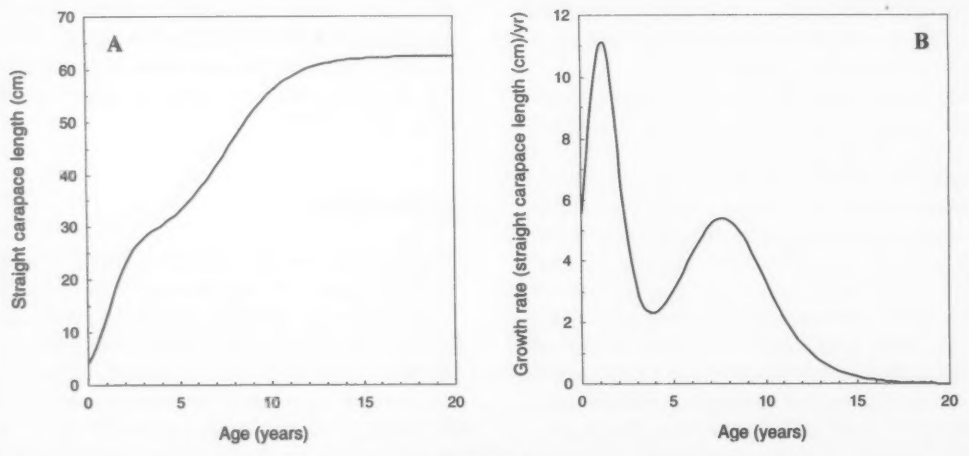

Figure 2

(**A**) Kemp's ridley sea turtle size (SCL cm) plotted as a function of the correction-factor age estimates derived from Zug et al. (1997). Solid curve shows the polyphasic logistic growth Equation 1 fitted to the growth data shown in Figure 1A, excluding the single outlier. (**B**) The age-specific growth-rate function for the Kemp's ridley sea turtle growth function shown in Panel A represented by the first derivative of Equation 1, which is $y'_{(t)} = \Sigma (\alpha_i \beta_i (\text{sech}^2 (\beta_i (t - \delta_i))))$ with the same parameters defined for Equation 1 and with sech (hyperbolic secant) = (1 – tanh).

function is inconclusive because the data span was incomplete, missing not only the first growth cycle (if it occurred at all) but also the onset of adult maturation. By the end of the study the remaining 8 turtles were still growing and below estimates of adult size (weight) recorded for wild stocks. Moreover, growth in captivity might well bear little similarity to the growth dynamics of wild stock Kemp's ridley sea turtles, which seem to grow much slower at a given size (Caillouet et al., 1986).

The nonparametric smooth shown here in Figure 1A fitted to a more complete age and size range for wild stock Kemp's ridley sea turtles implied that growth comprised two consecutive phases and that an explicit polyphasic model (Table 1; Fig. 2) might be a better parametric description of growth than monophasic models proposed previously for this species. Nonetheless, two major cautions are warranted prior to drawing further conclusions from Figure 2 about Kemp's ridley growth dynamics. These cautions relate to the implications for growth inferences due to 1) data sparsity in the early growth years for this data set and 2) the size composition anomaly between stranding subsamples for this data set.

The data were sparse in the lower region of the first inferred growth spurt (see Fig. 1). The growth-layer loss protocols used in deriving the skeletochronological age estimates provided differing coverage of this growth region (see Zug et al., 1997). The age estimates used in our study were based on the correction-factor protocol that was considered more reliable than ranking protocol estimates (Zug et al., 1997) despite providing no coverage of the first growth year except for hatchling size. The model that was fitted (Fig. 2A) interpolated between known hatchling age and the end of the first year on the basis of the explicit form implied by the specified parametric function (Eq. 1). Although the conclusion of the first growth phase completed by ca. 25–30 cm SCL (see Fig. 1A) is firm despite sparse data during early growth, a specific growth spurt ≥1 year of age is tenuous. Given the lack of data during the first year, maximum growth might just as feasibly occur immediately following hatching, resulting in a monotonic decreasing age-specific growth-rate function for the first cycle and not the nonmonotonic function seen in Figure 2B. On the other hand, a growth spurt might occur a little later after hatching, resulting in a nonmonotonic age-specific growth-rate function for the first cycle similar to that proposed in Figure 2B but with the spurt occurring at say 3 or 6 months rather than at 12 months of age. Because of a sparsity of data during the early growth years, all these growth scenarios for the first growth cycle are feasible; therefore data for the first 12 months of life following hatchling dispersal from the nesting beach are essential to resolve this important issue.

Nonetheless, other sources of information corroborate the growth profile proposed for the first phase in Figure 2B. First, the polyphasic function described by Equation 1 fitted the growth data well, including an estimated mean adult size (upper asymptote= $2(\alpha_1+\alpha_2)$=62.6 cm SCL from Table 1) consistent with empirical estimates of mean nesting female size of 64–65 cm SCL (Marquez, 1994). Moreover, the polyphasic function also predicted a mean hatchling size of 4.3 cm, which is consistent with the empirical estimate of mean hatchling size of 4.4 cm (Marquez, 1994). No other growth model has come close to predicting both the mean upper and lower size asymptotes of the postnatal development phase for the Kemp's ridley sea turtle. It is worth noting here that it is a common misconception in growth studies (particularly sea turtle growth studies) involving more than one animal that the upper asymptote of a parametric growth function estimates maximum adult size rather than the correct interpretation of mean adult size (see Ricker, 1979).

Second, a growth spurt ≥12 months of age and a growth phase completed by ca. 27 cm SCL (30–36 months of age) is coincident with developmental changes to the blood oxygen system of the Kemp's ridley sea turtle prior to acquisition of an adult blood system by 28 months of age (see Davis, 1991)—at least this was the case for captive-reared Kemp's ridley sea turtles. Davis (1991) also found that the oxygen capacity of the blood had increased substantially during the first 12 months of growth. The size range and timing of the first growth cycle is also consistent with apparent dietary and habitat shifts around 20 cm SCL (ca. 18 months of age: Fig. 2A; Eq. 1) from a presumed epipelagic habit to a coastal benthic habit (see Shaver 1991; Burke et al., 1994; Musick and Limpus, 1997).

The second major caution relates to a lack of informative cofactors (sex, geographic subsample) being included in the model because of insufficient records or small subsamples. For instance, sex was recorded for only 37% of the strandings, whereas the Atlantic coast subsample (cf. Gulf coast) accounted for 79% of the strandings data (see Fig. 1, B and C). Moreover, the Atlantic subsample comprised a significantly different size composition compared with that of the Gulf of Mexico (see Fig. 3). The apparent size composition anomaly might be due to 1) differential and inadequate spatial sampling of strandings and 2) developmental migration of Kemp's ridley sea turtles ≥40 cm SCL from the Atlantic coast to the Gulf of Mexico (see Collard and Ogren, 1990; Morreale et al., 1992; Epperly et al., 1995; Musick and Limpus,

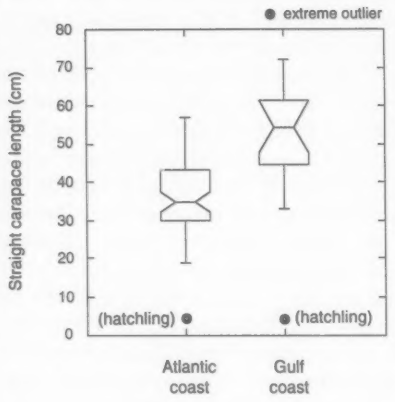

Figure 3

Boxplots of the size distribution of the Kemp's ridley sea turtle from the Atlantic Coast and Gulf of Mexico subsamples. The boxes show the interquartile range (25th to 75th percentiles), bars show 10th and 90th percentiles, and the notches show comparison-wise 95% confidence intervals. The notches on the two boxplots do not overlap each other, indicating a significant difference in median size between the two subsamples.

1997). If the Atlantic and Gulf coast subsamples in the Zug et al., (1997) data set represent two discrete populations with population-specific growth behaviors, then the growth model here (Table 1; Fig. 2) is applicable to the Atlantic group only although a similar polyphasic model is apparent for both subsamples despite a sparsity of data for the ≥50 cm SCL group of the Atlantic subsample (Fig. 1B) and ≤40 cm SCL group of the Gulf subsample (Fig. 1C). The inclusion of the Gulf subsample serves to provide sufficient data to derive the upper asymptote for estimating mean adult size (see Fig. 1C). The Atlantic subsample comprised only immature Kemp's ridley sea turtles consistent with recorded size distributions for populations resident in various habitats along the US Atlantic coast (see Burke et al., 1994, Epperly et al., 1995; Schmid, 1995).

If the Zug et al. (1997) data set is representative of a single panmictic interbreeding stock displaying some form of staged developmental migration, then the model presented here is a reasonable approximation of the growth dynamics of the endangered Kemp's ridley sea turtle. There is compelling support for this view given current knowledge of Kemp's ridley sea turtle movement patterns (Musick and Limpus, 1997). Further support comes from the discovery of a Kemp's ridley sea turtle (70 cm CCL, 67 cm SCL) nesting at Rancho Nuevo in 1996 (116 eggs laid) that had been tagged as a juvenile (51 cm CCL, 49 cm SCL) seven years earlier in Chesapeake Bay (Musick[1]). Growth for this nesting ridley was consistent with the polyphasic growth function (Fig. 2A) although clearly a single record is not sufficient to provide conclusive evidence. Nonetheless, if the Atlantic and Gulf subsamples represent a single panmictic interbreeding stock, then a juvenile growth spurt at 46 cm SCL (ca. 8 years old, Fig. 2B) would indicate an ontogenetic shift associated with developmental migration from juvenile foraging habitats in the South Atlantic Bight (Musick and Limpus, 1997) and from within the Gulf of Mexico (Collard and Ogren, 1990) to foraging grounds in habitats along the Gulf coast prior to the onset of sexual maturity.

It is also conceivable, given the dispersal scenarios proposed by Collard and Ogren (1990), that the Kemp's ridley sea turtle is a single panmictic interbreeding stock that comprises two distinct posthatchling developmental groups. One group remains within the Gulf of Mexico displaying relatively rapid growth owing to the warmer water (see Caillouet et al., 1995b). The second group represents the posthatchlings swept from the Gulf of Mexico that settle as juveniles (ca. 20 cm SCL) in the inshore developmental habitats of the mid-Atlantic (Morreale et al., 1992; Burke et al., 1994) and South Atlantic Bights (Epperly et al., 1995; Schmid, 1995). In this case the polyphasic growth model presented here (Table 1; Fig. 2) would be applicable to describing the mean stochastic growth dynamics of the cohorts swept each year from the Gulf of Mexico and undergoing growth in the Atlantic Bights prior to migrating back to the Gulf of Mexico. A separate growth model would need to be derived for the Gulf of Mexico developmental group although polyphasic growth behavior is also apparent for that subsample in our study (see Fig. 1C).

Clearly, a better understanding of the dispersal and developmental dynamics of the Kemp's ridley sea turtle based on a mark-recapture program with a high recapture likelihood is needed to resolve these complex issues. Although several local tagging programs have been undertaken (e.g. Caillouet et al., 1995a; Schmid, 1995; Burke et al., 1994, and references therein) a more comprehensive spatial and sampling-intensive program spanning the distributional range of this species is needed.

[1] Musick, J. 1997. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA. Personal commun.

Meanwhile, it is common practice to use somatic growth functions to estimate mean age at sexual maturity. The difficulty in using growth functions for this purpose is that there are no conclusive growth criteria to indicate onset of sexual maturity. Minimum or mean female nesting size, or an arbitrary size set slightly below mean nesting size, is a commonly used criterion. Using an arbitrary size criterion based on reasonable biological considerations, Caillouet et al., (1995b) proposed that head-started Kemp's ridley sea turtles irrespective of sex, took 10 years to reach sexual maturity at ca. 60 cm SCL. Zug et al. (1997) estimated 11–16 years for age-at-maturity for wild stock Kemp's ridley sea turtles on the basis of mean female nesting size. The upper asymptote of a parametric growth function is the correct estimate of mean adult size, if the correct growth function was used (see Ricker, 1979). By using the upper asymptote metric, it is then apparent that sexual maturity could be reached at ≥20 years of age for the current study (see Fig. 2B; Table 2) compared with 30 years of age for the Caillouet et al. (1995b) growth function (see Table 2).

But as Caillouet et al., (1995b) point out, mean adult size (nesting females) is a questionable criterion for estimating age at sexual maturity. That is why Caillouet et al. (1995b) defined an arbitrary size criterion to estimate age-at-maturity. However, the correct function for estimating mean age at maturity is an age-specific maturity-rate function conditioned on time-varying age, year, and cohort effects derived from a mixed longitudinal sampling study (see Chaloupka and Musick, 1997, for time-dependent demographic sampling issues). In the absence of such a complex function, a useful growth criterion for estimating age-at-maturity might be negligible growth derived from the age-specific growth-rate function indicating the onset of maturity. It is increasingly apparent that growth for sea turtles becomes negligible approaching the onset of sexual maturity (see Chaloupka and Limpus, 1997). Although this is a study-dependent and subjective metric, it is clear that negligible growth in the current study occurs ≥ 15 years of age or ≤ 0.25 cm SCL/year (see Fig. 2B and Table 2). Growth was imperceptible by 21 years of age (Table 2); thus the age range of 15–20 years appears to be a reasonable interval estimate of expected age at sexual maturity for the Kemp's ridley sea turtle.

It is therefore noteworthy that the Kemp's ridley sea turtle tagged in Chesapeake Bay as a juvenile (ca. 49 cm SCL) and discovered nesting seven years later at Rancho Nuevo (see "Discussion" above) was estimated by reference to Figure 2 to be about 9 years old when tagged and therefore 16 years old at the first recorded nesting. The nesting turtle was ca. 67 cm SCL, which is larger than the estimated upper asymptote of ca. 63 cm SCL (Table 1: $2(\alpha_1+\alpha_2)$ cm SCL). Recall, however, that the upper asymptote here represents mean adult size (or mean nesting size, assuming growth is not sex-specific); therefore 50% of a random sample of adult or nesting Kemp's ridley sea turtles would be >63 cm SCL ,whereas 50% of the sample would be smaller.

Despite sampling design constraints, cautions about skeletochronological methods, small sample size, and perhaps nonequivalent geographic subsamples, the data set presented in Zug et al. (1997) is of considerable importance for helping to improve our understanding of the growth dynamics of the endangered Kemp's ridley sea turtle. The re-analysis of these data with exploratory nonparametric smoothing suggested that expected age-specific growth for the Kemp's ridley sea turtle was polyphasic and could be modeled with a sequence of parametric curves. A parametric model comprising a summation of logistic functions fitted the data well, implying growth spurts at ≥1 year of age (mean size=13 cm SCL) and ca. 8 years of age (mean size=46 cm SCL) followed by negligible growth approaching the onset of maturity ca. 15–20 years of age (mean size=63 cm SCL). Polyphasic growth behavior is therefore one of many reasons why a monophasic growth function cannot fit the entire postnatal developmental phase of the Kemp's ridley sea turtle, let alone for any other sea turtle species (see Chaloupka and Musick, 1997).

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Age determination of larval strombid gastropods by means of growth increment counts in statoliths

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The queen conch, *Strombus gigas* Linnaeus, and the milk conch, *S. costatus* Gmelin, are important gastropods of the Caribbean region (Appeldoorn and Rodríguez, 1994). To age strombid larvae by means of their statoliths would be useful in order to study aspects of their larval life histories and ecology. Statoliths, like fish otoliths, are formed of aragonitic calcium carbonate deposited on a protein matrix and exhibit periodic growth increments (Radtke, 1983). Research on statolith microstructure has been limited primarily to age determination of commercially important cephalopods (e.g. Jackson, 1994). D'Asaro (1965) observed statocysts that appeared in four-day-old embryos of *S. gigas* and that were fully functional by day six; he also noted growth increments or rings on these structures. These increments were confirmed by Salley (1986). Our objective is to validate the use of statolith microstructure in *S. gigas* and *S. costatus* to provide information on age, growth, and length of larval life.

Materials and methods

Egg masses from eight *Strombus costatus* and one *S. gigas* were collected from ovidepositing females at a site 7 km south of La Parguera, southwest coast of Puerto Rico (17.92°N, 67.05°W). Egg masses were held in 75-L aquaria subjected to the natural light-dark cycle. Culture methods of Ballantine and Appeldoorn (1983) were used. Aquaria were cleaned daily, after which one liter of Tahitian *Isochrysis* (10^6 cells/mL) was added. A minimum daily sample of ten individuals was removed from each aquarium and preserved in 70% ethanol. We examined the statolith microstructure of larvae from the longest surviving cultures. Since no veligers reared in our laboratory developed through metamorphosis, we obtained preserved (5% buffered formalin, pH 8.0) *S. gigas* veligers and juveniles of known age from the Trade Wind Industries' hatchery in the Turks and Caicos Islands.

Preserved veligers were examined with a dissecting microscope, their larval shell length (apex to siphonal canal) was measured, and their shell removed. A drop of 60% solution of alizarin red in glycerin was added to increase contrast between stained soft tissues and the unstained statolith. Coverslips were added, sealed with Permount, and samples were inspected under a compound scope at 1,000×. Statolith diameters were measured with an ocular micrometer. Increments on statoliths were counted by focusing up and down through the statolith. For each day of age, counts were made from one statolith from each of 20 veligers; all counts were made by the same reader in a blind manner. General physical structure was observed and described, with emphasis placed on the periods preceding and following hatching, and, for *S. gigas* juveniles, preceding and following metamorphosis to determine the presence and nature of any transitional marks associated with these events.

Statolith diameter, number of growth increments, and shell length were averaged for each day and arranged with age (in days after hatching). Linear least-squares regressions were calculated to determine the relations among these three variables. To determine the precision (or reproducibility) of counts of increments (i.e. verification, Wilson et al., 1983), repeated counts for both statoliths were made on subsamples. The number of increments in these representative samples were counted three separate times (double-blind), and the results were averaged for individual veligers. Standard deviations (SD) were calculated for each individual; standard error of the means (SE) was calculated as appropriate. A nested analysis of variance (ANOVA) was done for each species to determine if variability in incremental counts was due to errors in measurement or to natural variability in increment deposition (Sokal and Rohlf, 1981). Data were grouped at four levels: 1) all

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individuals across age groups, 2) between individuals within age groups, 3) between statoliths within individuals, and 4) within statoliths.

For one culture of eight-day-old veligers of *S. costatus*, feeding was suspended for two consecutive days to induce change in statolith structure and to determine if changes in feeding regimen affected increment deposition. Statolith-increment numbers and statolith diameters (n=10) were compared with those of nonstarved larvae (n=10) of equivalent age with two-sample t-tests (Sokal and Rohlf, 1981).

Results

Statoliths from *Strombus costatus* and *S. gigas* veligers were similar in size, shape, and pattern of increment formation and were translucent in appearance. They have either a circular or elliptical appearance from a longitudinal view and a biconvex structure in transverse section. On the basis of changes in size and shape, three regions are apparent (Fig. 1). At the very center is a primordial granule, around which all other increments grow; newly hatched veligers show five increments (including the primordial granule). This five-increment region (region 1) is quite distinct because of its lighter color, greater width, and seemingly dome-like nature. Prehatching increments in *S. costatus* and *S. gigas* had mean widths of 1.11 µm and 1.22 µm, respectively. Deposited around region 1 is a second, slightly darker, region. Thinner and smaller in width, this region (region 2) is composed of increments formed between hatching and completion of metamorphosis. Increment widths corresponding to the first day after hatching averaged 0.33 µm for both *S. costatus* and *S. gigas*; over the first six days after hatching the average increment width was 0.24 µm for both species. A third region (region 3), observed only in juveniles of *S. gigas*, appears immediately after completion of metamorphosis. A darker band visible at the outer edge of region 2 results from the even smaller spacings between five or six increments deposited just before metamorphosis. Increments corresponding to the last day before metamorphosis (age 20 days) measured 0.09 µm on average, whereas increments corresponding to the first day after metamorphosis had a mean of 0.43 µm. Region 3 appears lighter than region 2, because of the wider increments.

In both species, most veligers hatched on the sixth day after egg mass deposition, defined as age 0. The mean number of increments on the first day after hatching was 6.00 for *S. costatus*, 6.70 for *S. gigas* (Table 1). Statoliths in *S. costatus* show a deposition pattern of 1.11 increments/day (SE=0.59) over days 0–11; in *S. gigas* the deposition rate was 1.13 increments/day (SE=0.59) over days 0–9 (Table 1). In *S. gigas* this pattern continued until metamorphosis. For the day preceding metamorphosis (age 20 days), mean number of increments was 26.05; two days after metamorphosis (age 23 days) mean increment number was 29.40 (Table 1).

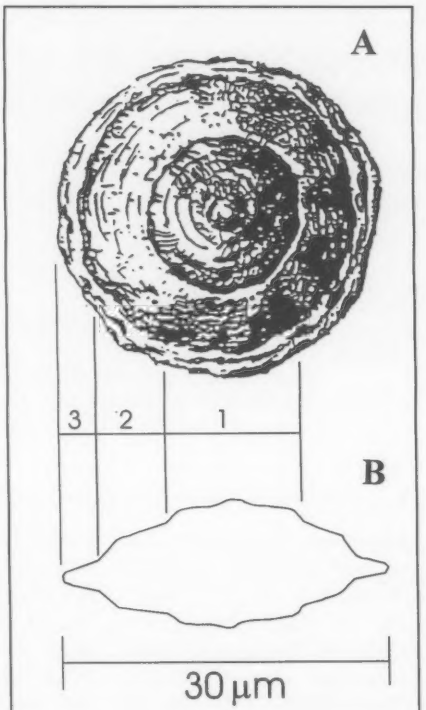

Figure 1

Generalized structure of *Strombus* statoliths: (**A**) longitudinal view; (**B**) inferred transverse view. Numbers identify the three morphological regions: 1 = prehatching, 2 = planktonic larva, and 3 = benthic postmetamorphic juvenile.

Significant regressions (P<0.05) were found between age (A, in days) and mean increment number (I) (*S. costatus*: $I = 6.08 + 0.986A$, r^2=0.98; *S. gigas*: $I = 6.17 + 0.984A$, r^2=0.99; data from Table 1). For analysis of *S. gigas*, we pooled locally-reared larvae with those brought from the Turks and Caicos. Separate regressions for these two sets of larvae were not significantly different. In the regression equations for both species, the slope did not differ from 1 significantly and the intercept did not significantly differ from 6 (t-test, P<0.05). Thus, the equations can be generalized to predict strombid veliger age from the number of statolith increments: $A = I - 6$.

Table 1

Mean statolith diameter (μm ± SD), mean number of increments (± SD) and mean shell length (μm ± SE) by age (days after hatching) for *Strombus costatus* and *S. gigas*. n = 20 for each day. META = day of metamorphosis, data not available.

	Strombus costatus			*Strombus gigas*		
Age (d)	Statolith diameter	Number of increments	Shell length	Statolith diameter	Number of increments	Shell length
0	13.35 ± 0.48	6.00 ± 0.65	345.00 ± 32.60	14.65 ± 0.80	6.70 ± 0.73	325.00 ± 35.36
1	14.05 ± 0.22	7.06 ± 0.64	390.00 ± 13.69	15.05 ± 0.59	7.30 ± 0.66	375.00 ± 40.82
2	15.30 ± 0.56	8.80 ± 0.70	440.00 ± 13.69	15.70 ± 0.71	7.25 ± 0.79	387.50 ± 17.68
3	15.50 ± 0.50	8.75 ± 0.50	470.00 ± 18.71	16.45 ± 0.50	8.00 ± 1.03	408.25 ± 14.43
4	15.93 ± 0.46	9.57 ± 1.28	625.12 ± 17.83	—	—	—
5	—	—		16.35 ± 0.51	10.72 ± 0.46	443.00 ± 18.32
6	16.14 ± 0.64	11.71 ± 0.73	625.80 ± 21.77	17.40 ± 0.97	12.35 ± 1.26	458.25 ± 28.87
7	15.65 ± 0.91	12.65 ± 1.04	635.00 ± 15.69	17.15 ± 0.57	13.45 ± 1.28	461.35 ± 15.22
8	16.50 ± 0.67	14.85 ± 0.99	641.75 ± 30.28	—	—	—
9	—	—		18.10 ± 0.30	15.55 ± 2.63	466.75 ± 14.43
10	16.35 ± 0.57	15.15 ± 2.03	650.00 ± 14.42	17.93 ± 0.46	17.07 ± 1.59	475.80 ± 13.67
12	17.33 ± 1.55	18.33 ± 1.15	700.67 ± 24.32			
19				27.60 ± 0.82	24.35 ± 0.75	1160.00 ± 31.75
20				27.90 ± 0.55	26.05 ± 0.83	1177.50 ± 40.00
21				META	META	META
22				28.15 ± 1.39	26.75 ± 4.28	1340.00 ± 44.50
23				30.45 ± 1.10	29.40 ± 1.10	1655.00 ± 83.25

Individual statolith increment counts and the magnitude of corresponding standard deviations (Tables 2 and 3) indicate that observed variability may be due to errors in measurement, not to variability in increment deposition. Nested ANOVA of subsamples of each species supported this hypothesis (Table 4), showing significant variability only at the level of readings between age groups.

Within each species, the relation between age (A) and statolith diameter (D, μm) was more variable than that between age and increment count (*S. costatus*: $D = 14.21 + 0.26A$, $r^2 = 0.80$; *S. gigas*: $D = 14.93 + 0.34A$, $r^2 = 0.93$). Similarly, the relation between age and shell length (L, μm) was more variable than that between age and increment count but was similar to that between statolith diameter and age (*S. costatus*: $L = 397.6 + 29.2A$, $r^2 = 0.83$; *S. gigas*: $L = 356.7 + 13.7A$, $r^2 = 0.89$).

Significant regressions occurred between shell length and statolith diameter (*S. costatus*: $L = -1015 + 100.4D$, $r^2 = 0.85$; *S. gigas*: $L = -237 + 39.9D$, $r^2 = 0.90$). Data for *S. gigas* obtained from the Turks and Caicos hatchery did not, however, fit this relation, suggesting that 1) environmental or genetic factors influence the relative growth of these structures, or 2) the relation is not linear over the entire larval and postmetamorphic period.

Larvae of *S. costatus* subjected to starvation showed no unusual pattern in region 2; mean number of increments between seven-day-old starved (12.09 ± 0.74 SD) and nonstarved (12.65 ± 1.04 SD) larvae were not significantly different ($t_{18} = 0.262$; $P > 0.05$). Mean statolith diameter was also similar in the two groups (15.65 ± 0.91 SD μm for nonstarved larvae; 14.83 ±0.75 SD μm for starved ones) ($t_{18} = 1.414$; $P > 0.05$).

Discussion

Statoliths of strombid larvae have a distinctly recognizable structure at hatching. Region 1 consists of a primordial granule surrounded by four increments. Three regions within the statolith result from changes in density of increments caused by abrupt changes in increment width at times of hatching and metamorphosis. Large transitions in incremental width may be caused by differences in metabolism during normal larval growth and development, including variable mineral deposition in the larval shell (Maeda-Martínez, 1987).

In both *S. costatus* and *S. gigas*, the rate of increment formation is constant after hatching. Variability found in incremental deposition was due largely to errors in measurement, not variation in depositional rate. A two-day period of starvation did not produce any noticeable structural change or precise mark. Starved veligers may have continued growing on stored energy reserves (Rodríguez Gil, 1995), negating differences between treatments. That starved

veligers still produced statolith rings without structural change implies that age estimates of veligers from statolith increment counts are robust. Periodicity of statolith growth in larval *S. costatus* and *S. gigas* is sufficiently reliable to be considered a better tool for age determination than diameter of statolith or measurement of shell length. Counts of increments were measurably less variable with age than were measurements of statolith diameter, or shell length.

In fishes, otoliths have been used to address questions regarding larval dispersal (Thresher and Brothers, 1985); settlement dynamics (Victor, 1983); growth rates (Radtke and Dean, 1982); mortality rates (Essig and Cole, 1986); and larval patch-size estimation (Victor, 1984). Statolith-based age and growth determination, however, has not been used in early life history studies of mollusks; characteristics such as size, shell structure, and distance offshore have been used to infer relative age or length of planktonic life (e.g. Scheltema, 1978; Jablonski and Lutz, 1980, 1983; Pechenik et al., 1984; Pechenik, 1986). Our results here indicate a more highly quantitative method for ageing larvae.

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Table 2

Variability in statolith increment counts within laboratory-reared larval *Strombus costatus*. Age = days after hatching.

	Statolith A					Statolith B				
	Counts					Counts				
Age (d)	1	2	3	Mean	SE	1	2	3	Mean	SE
0	6	6	6	6.00	0.00	6	5	5	5.33	0.58
0	6	6	6	6.00	0.00	5	5	5	5.00	0.00
0	6	7	7	6.67	0.58	7	7	6	6.67	0.58
(average)				6.22	0.44				5.67	0.87
1	6	6	6	6.00	0.00	7	7	7	7.00	0.00
1	7	7	8	7.33	0.58	8	6	8	7.33	1.15
(average)				6.67	0.82				7.17	0.75
2	8	8	9	8.33	0.58	9	9	9	9.00	0.00
2	10	8	9	9.00	1.00	9	9	9	9.00	0.00
2	9	9	9	9.00	0.00	10	10	8	9.33	1.15
(average)				8.78	0.67				9.11	0.60
4	10	10	10	10.00	0.00	10	9	9	9.33	0.58
6	11	12	11	11.33	0.58	12	13	12	12.33	0.58
6	11	11	11	11.00	0.00	11	12	11	11.33	0.58
(average)				11.17	0.41				11.83	0.75
7	10	10	11	10.33	0.58	11	11	12	11.33	0.58
7	13	11	13	12.33	1.15	12	10	13	11.67	1.53
7	14	14	12	13.33	1.15	15	13	13	13.67	1.15
7	14	14	15	14.33	0.58	15	13	13	13.67	1.15
(average)				12.58	1.73				12.58	1.51
8	15	14	15	14.67	0.58	14	13	16	14.33	1.53
8	13	15	14	14.00	1.00	12	14	13	13.00	1.00
(average)				14.33	0.82				13.67	1.37
10	15	14	14	14.33	0.58	16	15	15	15.33	0.58
10	14	16	15	15.00	1.00	15	14	16	15.00	1.00
(average)				14.67	0.82				15.17	0.75

Table 3

Variability in statolith increment counts within laboratory-reared larval *Strombus gigas*. Age = days after hatching.

	Statolith A					Statolith B				
	Counts					Counts				
Age (d)	1	2	3	Mean	SE	1	2	3	Mean	SE
0	6	6	6	6.00	0.00	6	6	7	6.33	0.58
0	8	8	7	7.67	0.58	8	8	7	7.67	0.58
0	7	7	7	7.00	0.00	7	6	7	6.67	0.58
(average)				6.89	0.78				6.89	0.78
1	8	7	7	7.33	0.58	8	7	6	7.00	1.00
1	8	7	7	7.33	0.58	9	8	7	8.00	1.00
1	7	8	7	7.33	0.58	8	8	8	8.00	0.00
(average)				7.33	0.50				7.67	0.87
2	8	6	7	7.00	1.00	7	7	7	7.00	0.00
2	7	7	6	6.67	0.58	7	6	7	6.67	0.58
(average)				6.83	0.75				6.83	0.41
3	7	7	6	6.67	0.58	7	7	7	7.00	0.00
5	11	11	11	11.00	0.00	11	11	11	11.00	0.00
5	10	11	10	10.33	0.58	10	10	11	10.33	0.58
(average)				10.67	0.52				10.67	0.52
6	13	15	13	13.67	1.15	12	14	14	13.33	1.15
6	10	11	11	10.67	0.58	11	12	12	11.67	0.58
(average)				12.17	1.83				12.50	1.22
7	14	14	12	13.33	1.15	14	12	11	12.33	1.53
7	12	12	12	12.00	0.00	12	13	13	12.67	0.58
7	14	16	15	15.00	1.00	16	13	14	14.33	1.53
(average)				13.44	1.51				13.11	1.45
9	18	17	15	16.67	1.53	16	20	16	17.33	2.31
9	16	15	17	16.00	1.00	16	18	16	16.67	1.15
9	14	14	14	14.00	0.00	13	15	13	13.67	1.15
(average)				15.55	1.51				15.89	2.20
10	16	18	17	17.00	1.00	20	20	19	19.67	0.58

Table 4

Nested ANOVA of statolith increment counts for subsamples of laboratory-reared larval *Strombus costatus* and *S. gigas*. SS = sum of squares, df = degrees of freedom, MS = mean square, P = probability of error, S = $P \leq 0.05$, NS = $P > 0.05$.

Source	SS	df	MS	F-ratio	P
Strombus costatus:					
Among age groups	6,868.3	7	981.2	103.3	$P<0.05$ S
Among individuals	171.5	18	9.5	5.3	$P>0.05$ NS
Between statoliths	68.1	37	1.8	0.2	$P>0.05$ NS
Within statoliths	1,063.4	123	8.7		
Total	8,171.3	185	44.2		
Strombus gigas:					
Among age groups	6,732.5	8	841.6	195.7	$P<0.05$ S
Among individuals	81.7	19	4.3	10.8	$P>0.05$ NS
Between statoliths	14.1	39	0.4	0.7	$P>0.05$ NS
Within statoliths	74.8	119	0.6		
Total	6,885.2	185	37.2		

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Bias in Chapman-Robson and least-squares estimators of mortality rates for steady-state populations

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When age-frequency data are insufficient for fisheries scientists to estimate year- or age-specific mortality, they are often pooled to provide a single estimate for all fully recruited age groups. The accuracy of a pooled estimate depends largely on whether or not the sampled population is in a steady state, i.e. a state in which the rates of recruitment and mortality are relatively constant with respect to time and age. Departures from this condition introduce known biases to the estimate of mortality (Ricker, 1975; Jensen, 1984). These departures may be difficult to detect because trends in time-specific recruitment or time- and age-specific mortality can result in a population age structure that is quite similar to that for a steady-state population. For instance, a long-term increasing trend in recruitment could result in a stable age frequency that would indicate a higher mortality rate than was actually occurring (for various scenarios see Ricker, 1975).

Pooled-data estimation techniques that have been applied to age-frequency data for fish populations include "catch curve" least-squares regression analysis (Seber, 1973; Ricker, 1975) and nonregression-based methods developed by Heincke (1913), Jackson (1939), and Chapman and Robson (1960). Of the nonregression-based estimators, the Chapman and Robson estimator is preferred because it is the least sensitive to sampling error (Robson and Chapman, 1961). Despite the restrictive steady-state requirements, these techniques have been applied to a wide variety of marine animals; recent examples include Atlantic croaker, *Micropogonias undulatus* (Barbieri et al., 1994); blue rockfish, *Sebastes mystinus* (Adams and Howard, 1996); red drum, *Sciaenops ocellatus* (Ross et al., 1995); red porgy, *Pagrus pagrus* (Pajuelo and Lorenzo, 1996); and deep-water shrimp, *Aristeus antennatus* (Ragonese and Bianchini, 1996).

The Chapman-Robson (CR) estimator is based on the probability density function of the geometric distribution and provides a unique minimum-variance, unbiased estimate of survival (S),

$$S = \frac{\sum_{i=1}^{N} x_i}{N + \sum_{i=1}^{N} x_i - 1},$$

where x_i = the number of years the ith fish is older than the age at full recruitment; and
N = the total number of fully recruited fish.

The underlying assumption is that the age of each fish sampled represents a random, independent age observation from a steady-state population. For age-frequency data that have been truncated to eliminate some older age groups, a slightly biased maximum likelihood estimator of survival (CRt) that can be solved by iteration is

$$\frac{\sum_{i=1}^{N} x_i}{N} = \frac{S}{1-S} - (K+1)\frac{S^{(K+1)}}{1-S^{(K+1)}},$$

where $K + 1$ = the number of fully recruited age groups used (Chapman and Robson 1960).

The least-squares regression (LS) estimator provides an unbiased estimate of $-\log S$ (denoted as Z, the instantaneous total mortality rate) and is based on a linear fit to a log-transformed exponential decay model

$$\mathrm{E}(\log N_j) = \log(pN_0) - Zj,$$

where N_j = the number of age j fish in the sample;
N_o = the original number of fish in the population; and
p = the probability that a fish in the population is included in the sample (Seber, 1973).

As required for linear regression, log-abundance data are assumed to be independent and normally distributed with constant variance along the regression line. Concern about violating these assumptions led Chapman and Robson (1960) to recommend that when the LS method is used, the age-frequency data should be truncated to exclude less abundant age groups.

Although both the CR and LS estimator returned very accurate estimates of Z for a suite of exact steady-state age frequencies (Jensen, 1985), the effect of random variation within the sample age frequencies

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has not been investigated. Jensen (1996) found that the CR method was less biased and more precise than the LS method when used to estimate mortality from the age structure of pooled, simulated net-hauls of lake whitefish, *Coregonus clupeaformis*. A random sample drawn from a known geometric distribution of ages will have an age distribution that varies stochastically from the true distribution. In this study, I evaluate the effect of sample size, mortality rate, and an age-frequency truncation scheme on the accuracy and precision of the CR (and CRt) and LS estimators when the sample age frequency is drawn randomly from a population of geometrically distributed ages.

Materials and methods

I used a stochastic model that allowed for random departures from the exact age distribution of the population to generate the simulated sample age frequencies. Under a known, constant survival rate, a geometric distribution function defines the cumulative probability of a fish from a fully recruited cohort being less than age j as

$$P(age < j) = \begin{cases} 0 & j < 1 \\ \sum_{m=1}^{j} (1-S)S^{m-1} & j \geq 1, \end{cases}$$

where S = the annual survival rate.

For this simulation, age-0 fish are defined as those in their first year of full vulnerability to capture. I sampled individual aged fish from this distribution by choosing a random, uniform number (probability) within the interval from 0 to 1 and determining the age corresponding to this value of the cumulative distribution function. By repeating this process, I was able to draw randomly a specified number of aged fish from a known geometric distribution defined by S. Each generated sample consisted of 100–1,000 individuals drawn independently from geometric distributions defined by Z values between 0.20 and 2.00. One thousand simulations were run for each combination of sample size and Z. For each simulation, a CR estimate of S and an LS estimate of Z were calculated from the sample age frequency. Means of the Chapman-Robson estimates of S were converted to Z so that they could be compared to the means of the LS estimates of Z.

The effect of constraining the right-hand limb of the sample age frequency was investigated by truncating each age-frequency distribution and recalculating mortality. The CRt and the LS estimates were calculated with these data, and the mean CRt estimates of S were converted to Z. Each truncated age frequency was a subset of a simulation from the complete age-frequency simulations in which all fish that were older than the oldest age group meeting or exceeding a threshold abundance of 5 fish were removed. Although this truncation scheme reduced the effective sample size within each simulation, it accurately reflected the application of a truncation scheme to a real sample.

Results and discussion

Simulations indicated that mean CR estimates of mortality for the complete age frequencies were essentially unbiased. At all Z's and sample sizes examined, the mean CR estimator agreed closely with the true value of Z. All differences between estimated mean Z's and true Z's (relative to the true Z) were <1% (Table 1).

The maximum likelihood estimator developed for use with truncated age frequencies (CRt) showed a negative bias that was greatest when sample size was low. With a 5-fish threshold rule, the mean CRt estimate of instantaneous total mortality was biased –12% at $Z = 0.2$ for a random sample of 100 fish (Fig. 1). At sample sizes of 300 fish or more, bias was reduced to less than about –4% for all Z's (Fig. 1).

The mean LS estimates of Z for complete age frequencies were consistently less than the true instantaneous total mortality rate. This bias was greatest at low levels of Z when sample sizes were small (Table 2). At $Z = 0.2$, the difference between the mean estimated Z and true Z ranged from –16% for samples of 1,000 individuals to –37% for samples of 100. Deviations were much less, –4% to –8%, for all sample sizes when the true Z was 2.0. Bias in the LS estimator was reduced by truncating the sample age frequency. When I used a minimum threshold abundance of five, the negative bias was reduced to less than about 5% at sample sizes of at least 200 fish (Fig. 1).

Precision of the CR and CRt estimators was generally better than that of the LS estimator, especially at low Z's. Although precision improved for all estimators as sample sizes became larger, the coefficient of variation (CV) for the CR and CRt estimators approached 1% for large samples at $Z = 0.2$, whereas the CV for the LS estimator approached only 6–9% (Fig. 2). For all given sample sizes, the precision of the CR and CRt estimators deteriorated as Z increased. The precision of the LS estimator changed little as Z increased, except when the estimator was based on samples of only 100 fish. In general, the CV's for the CR or CRt estimators were less than the

Table 1

Percent deviation from true instantaneous total mortality rate (Z) for the mean of 1,000 Chapman-Robson estimates of Z for each of the given combinations of sample size and true Z. Frequencies for all age groups were used in calculating mortality rates.

	Sample size									
True Z	100	200	300	400	500	600	700	800	900	1,000
0.20	–0.2	–0.1	–0.2	0.1	–0.0	–0.0	0.1	0.2	0.1	–0.0
0.40	–0.1	0.0	0.2	–0.1	0.3	–0.1	0.1	0.2	–0.2	0.2
0.60	–0.3	–0.2	0.0	0.0	–0.1	–0.0	–0.2	0.0	–0.2	0.1
0.80	–0.1	–0.2	0.2	–0.1	0.0	0.2	0.1	–0.0	–0.1	0.0
1.00	0.4	0.2	0.4	–0.1	–0.0	0.1	0.1	0.1	0.0	–0.2
1.20	–0.5	0.2	0.1	–0.0	0.1	0.0	0.2	–0.0	–0.2	–0.1
1.40	–0.3	0.3	–0.1	0.1	0.0	–0.0	–0.1	–0.1	0.0	–0.1
1.60	0.6	–0.1	0.2	0.2	0.2	–0.2	0.1	–0.1	–0.1	–0.1
1.80	–0.2	0.1	0.1	–0.1	0.1	–0.2	–0.1	0.1	–0.2	0.2
2.00	–0.1	–0.0	0.3	–0.1	0.0	–0.2	–0.2	–0.1	0.2	0.2

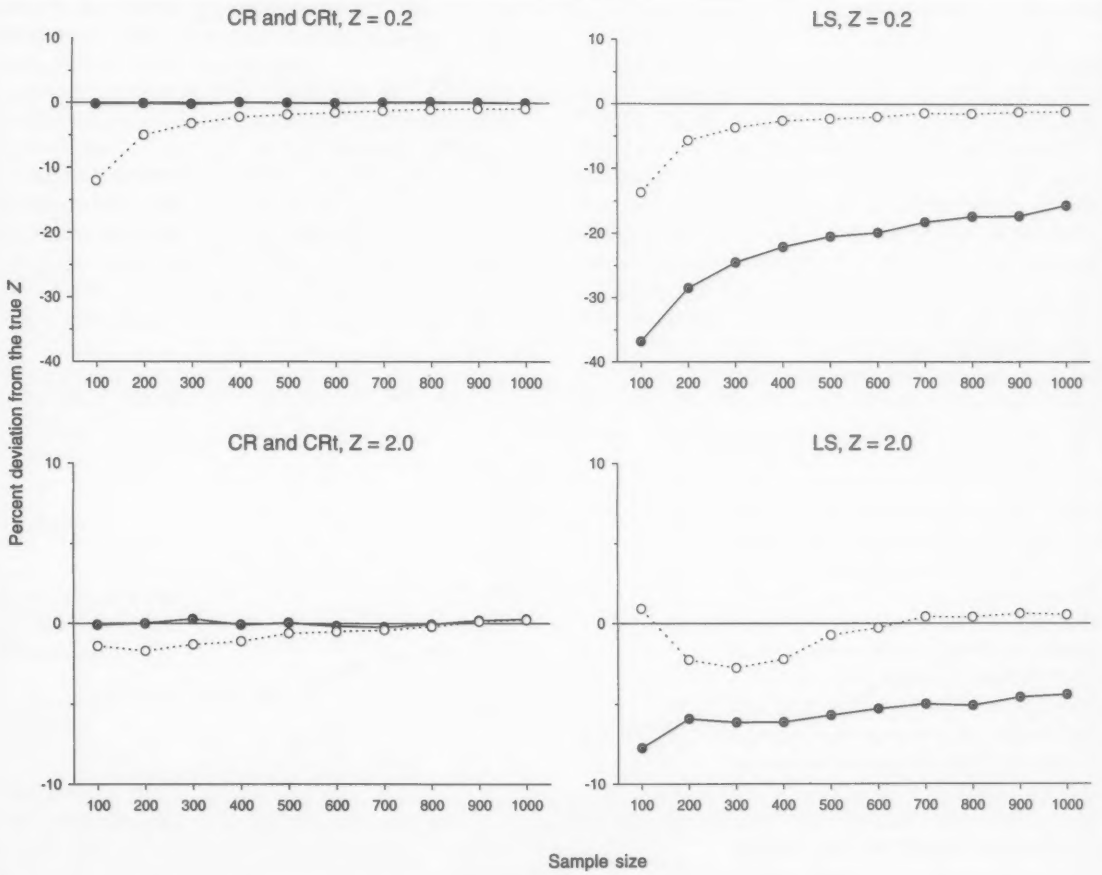

Figure 1

Percent deviation from true instantaneous total mortality (Z) for the mean of 1,000 Chapman-Robson (CR) or Chapman-Robson-for-truncated-data (CRt) estimates of survival or least-squares regression (LS) estimates of equivalent Z for different sample sizes when true Z is 0.2 or 2.0. The threshold levels, representing the minimum acceptable abundance for the oldest age used in the calculation of mortality were one fish (—●—) and five fish (—○—).

Table 2

Percent deviation from true instantaneous total mortality rate (Z) for the mean of 1,000 least–squares regression estimates of Z for each of the given combinations of sample size and true Z. Frequencies for all age groups were used in calculating mortality rates.

	Sample size									
True Z	100	200	300	400	500	600	700	800	900	1,000
0.20	–36.8	–28.5	–24.6	–22.1	–20.5	–19.9	–18.2	–17.4	–17.3	–15.6
0.40	–25.2	–20.4	–18.3	–16.9	–14.7	–14.3	–14.3	–13.2	–13.2	–12.3
0.60	–19.6	–17.1	–14.0	–12.9	–12.9	–11.9	–11.5	–11.3	–10.7	–10.6
0.80	–15.8	–14.1	–11.3	–11.0	–10.3	–9.8	–9.6	–9.3	–9.2	–9.7
1.00	–13.6	–10.7	–9.5	–9.3	–8.7	–9.1	–8.3	–7.8	–7.9	–7.9
1.20	–13.0	–9.1	–9.2	–8.4	–7.3	–8.2	–7.5	–7.2	–7.3	–6.8
1.40	–10.8	–9.1	–7.5	–7.9	–6.6	–6.8	–6.6	–6.5	–5.9	–7.1
1.60	–8.8	–7.6	–6.9	–6.2	–6.0	–7.0	–5.9	–5.6	–5.7	–6.1
1.80	–8.3	–6.7	–7.2	–6.4	–5.5	–5.1	–4.4	–5.6	–4.8	–4.9
2.00	–7.7	–5.9	–6.1	–6.1	–5.7	–5.3	–5.0	–5.1	–4.6	–4.4

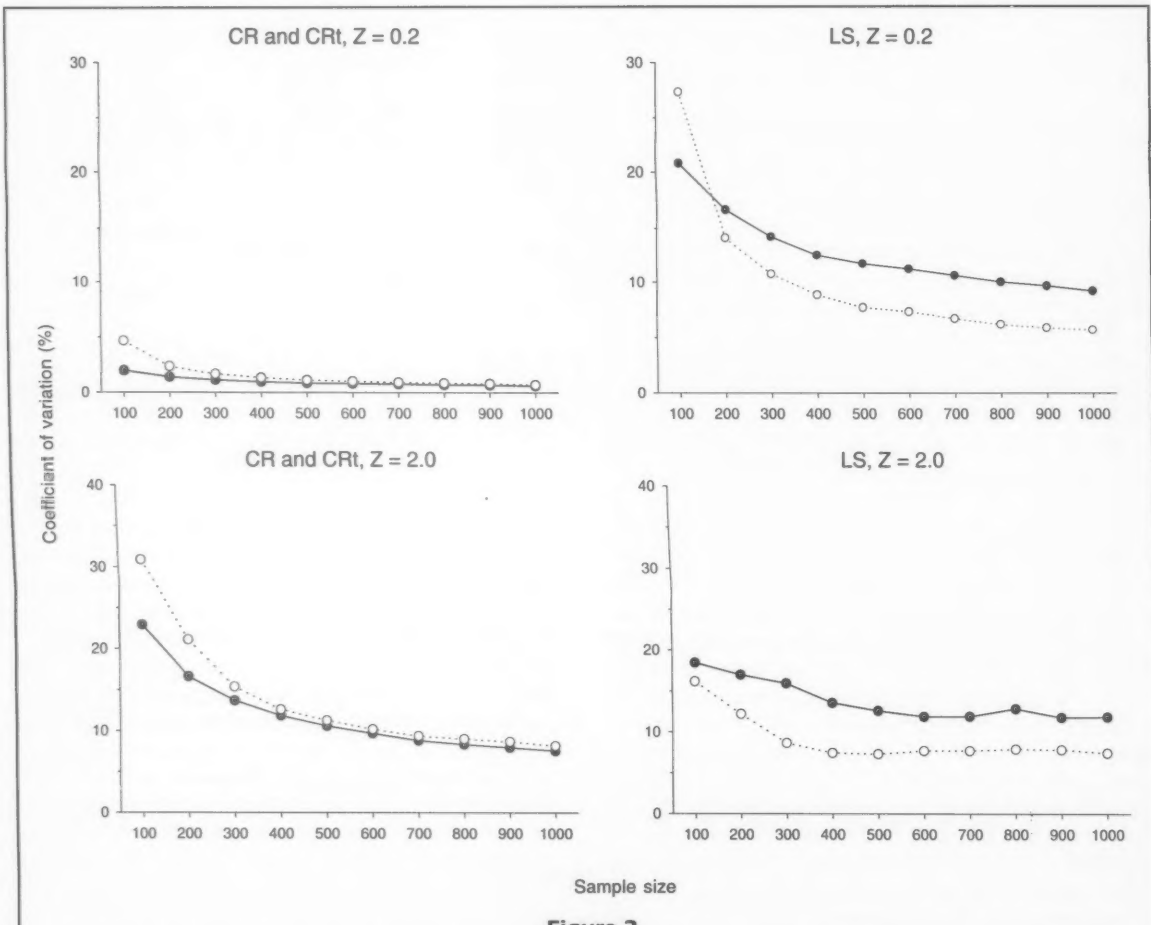

Figure 2

Coefficients of variation for Chapman-Robson (CR) and Chapman-Robson-for-truncated-data (CRt) estimates of survival or least-squares regression (LS) estimates of equivalent instantaneous total mortality (Z) made from samples of 100 to 1,000 ages generated stochastically under $Z = 0.2$ or $Z = 2.0$. Complete age frequencies (—●—) or those truncated using a 5-fish threshold (—○—) were used.

CV's for the LS estimator when Z was low but were similar or higher when Z was high.

When all fully recruited fish are equally available to a sampling gear, the CR estimator can provide a more accurate estimate of mortality than the LS estimator can. Applying the least-squares estimator to these data clearly violates the linear-regression assumption of equal variances among age groups. When a population is subjected to a low Z, the frequency distribution of log-abundances for older age groups in a sample becomes skewed to the right because log-abundance reaches a lower limit at zero (log of 1; Fig. 3). The frequency distribution of log-abundance then becomes truncated (undefined) past some distance to the left of its mean when zero abundances occur in the untransformed frequencies. The variances of the log-abundances appear to be positively related to age until the log-abundance frequencies become truncated when zero abundances appear in the samples for older age groups.

Empirical evidence led Chapman and Robson (1960) to conclude that haul data (catch rates for each age group) had an approximately constant variance when log transformed. However, the results from my simulations indicate that variances for the log-abundances are likely to differ among age groups. The assumption of constant variance is likely to be met only when the sampling gear operates on a few abundant age groups, in which there is no chance of only periodically encountering an older age group. This led Chapman and Robson (1960) to suggest that these data should be truncated to eliminate the age frequencies beyond the oldest age with a minimum abundance of five fish. Although my findings concur with those of Chapman and Robson, the use of this threshold rule to eliminate older age groups does not completely eliminate all bias in the LS estimator—bias that can be attributed to violations of the assumptions on which the linear regression is based.

For truncated age-frequency data, both estimators gave biased results when small samples were drawn from a population of many age groups (Z=0.2). In these cases, truncation generally resulted in smaller samples that had far fewer age groups than were in the original complete age frequency. At high Z's, age-frequency truncation reduced bias in the LS estimator to less than 5% at all sample sizes and reduced bias in the CRt estimator to less than 2%.

Violations of steady-state assumptions probably impart the most serious biases to pooled estimators of mortality. By simply inspecting a plot of log-abundance versus age for evidence of concavity or for a trend in the linear regression residuals, one can detect gross violations to these assumptions. Subtle biases inherent when the assumptions required by linear regression are not met are more difficult to detect. Both the CR and LS methods can provide very accurate and precise estimates of Z for age frequencies that follow an exact geometric distribution (Jensen, 1985). However, the LS estimator is biased when sample ages are drawn randomly from a steady-state, geometrically distributed population, whereas the CR estimator is not. The LS estimator may be more robust when age samples are not taken randomly (Chapman and Robson, 1960). The CRt and LS estimators generally showed similar levels of bias when the sample age structure is truncated with a minimum frequency criterion of 5 fish. In summary, the CR estimator will provide a more accurate and at least as precise an estimate of mortality as the LS estimator will when a random and complete age-frequency sample can be obtained from a population in steady-state.

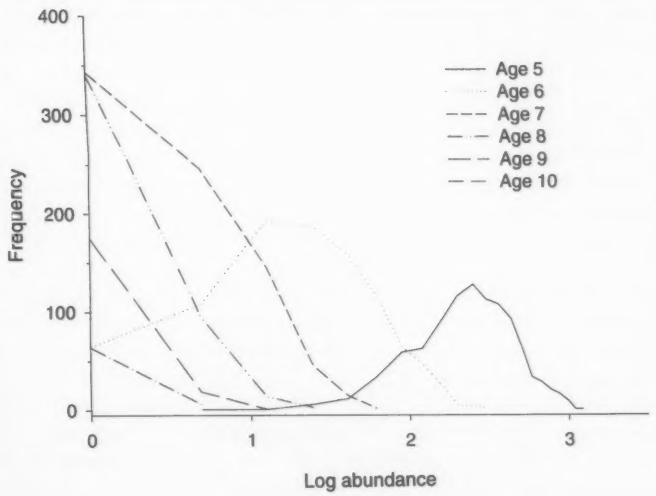

Figure 3

Frequency distributions of log-abundance for ages 5–10 generated stochastically with Z = 1.0. Log-abundance of each age group was taken from 1,000 simulations in which samples of 1,000 ages were drawn during each simulation.

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The effects of formalin and freezing on ovaries of albacore, *Thunnus alalunga*

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In almost every biological sampling program, tissue samples are collected and preserved for further examination. In this study, the effects of freezing and 10% buffered formalin on albacore, *Thunnus alalunga,* ovaries are compared to examine how each method of preservation affects ovarian weight and oocyte diameter. Formalin is frequently used to preserve ovaries for histological studies but, due to its toxicity, it may not be a good choice in all cases, and alternative methods, such as freezing, should be investigated. There is limited information on the effects of preservation on tuna gonads and, specifically, on albacore gonads. We investigated the effects caused by freezing and 10% buffered formalin on weight and oocyte diameter, because weight and other measurements (such as oocyte diameter) from fresh samples are not considered interchangeable with those from preserved samples (Lagler, 1968).

The purpose of our investigation was to compare fresh ovarian weights with weights of frozen ovaries and formalin-preserved ovaries from albacore as well as to determine how the diameters from oocytes are affected by differing methods of preservation.

Materials and methods

Albacore are seasonal spawners, spawning mainly during summer months (Otsu and Uchida, 1959; Ramon and Bailey, 1996). Ovaries were collected from albacore caught from 1990 to 1993 (Table 1) with longline gear in the South Pacific (group A) and in waters off Hawaii (group B) and with trolling gear in the North Pacific (group C). In group B, samples were labeled as one of three subgroups (B1, B2, or B3) on the basis of the method of preservation used (Table 1).

In the South Pacific, ovaries from each collected fish were dissected and preserved; a total of 150 pairs were collected. In the North Pacific, sampling took place at two sites: 1) between latitude 42°33'N and 52°02'N and from longitude 129°00'W to 145°52'W and 2) in the waters off Hawaii. Table 1 lists the methods of preservation used for all samples.

To investigate the effects that freezing and 10% buffered formalin have on oocyte diameter, we examined oocyte diameters from 58 immature North Pacific albacore from 70 cm to 89 cm fork length (FL) in group C. Right-side ovaries were preserved in 10% buffered formalin; left-side ovaries were frozen until processed two months later. The diameters of the most developed oocyte for each side of the ovary were measured to the nearest 0.01 mm and compared statistically with Student's *t*-test.

To compare differences in oocyte diameter and weight between the two methods of preservation, we used ovaries from subgroup B, which consisted of large, mature albacore (>95 cm FL). The mean diameter of oocytes in the most developed mode was measured from each side of the ovary and compared statistically with Student's *t*-test. The most developed mode of oocytes was determined with the criteria and method described by Schaefer (1987).

The effect of preservation on ovarian weight was examined for all samples collected in Hawaii (group B). Ovaries in group B were weighed fresh to the nearest 0.1 g and were then either preserved in 10% buffered formalin or were frozen. The samples were then reweighed two to three months later; samples preserved in 10% buffered formalin were placed on a paper towel, and excess moisture was patted off before they were weighed to the nearest 0.1 g on a Mettler PM3000 electronic balance. Frozen samples were thawed before being placed on a paper towel, and excess moisture was patted off before they were weighed.

The preserved weights of ovaries were compared with fresh weights by means of Student's *t*-test.

Results and discussion

Effect of preservation on oocyte diameter

Because measurements of oocyte diameter were not made on fresh oocytes, we assumed that left and right ovaries develop at the same rate. This assumption was tested with preserved specimens. Mean oocyte diameters of oocytes in the most developed mode in the right and left ovaries in group A were compared with mean oocyte diameters of oocytes in subgroups B2 and B3. The results indicated no

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Table 1

Summary of albacore ovaries collected in the Pacific Ocean and preservation treatment used. MFL = Mean fork length.

Group	Location	Date	Number of samples	Collection purpose	Preservation method
A—South Pacific	New Caledonia lat. 21–23°S long. 164–166°E	May 1990–Feb 1992	105	Control group for oocyte diameter MFL = 90 cm (78–103 cm)	Formalin
	Tonga lat. 16–29°S long. 171–177°W	Jan 1990–Feb 1992	45	Control group for oocyte diameter MFL = 88 cm (82–102 cm)	Formalin
B—North Pacific	Hawaii within 200-mi EEZ	Jun 1991–Aug 1992	95	Preservation effects on weight and oocyte diameter MFL = 103 cm (96–116 cm)	
B1			16	Left and right ovary of each pair treated differently	Formalin or Frozen
B2			64		Formalin
B3			15		Frozen
C—North Pacific	U.S. jigboat fishery lat. 42–53°N long. 129–146°W	Aug 1990–Sep 1990	60	Preservation effects on oocyte diameter MFL = 82 cm (78–87 cm) Left and right ovary of each pair treated differently	Formalin or Frozen

Table 2

Mean oocyte diameter (mm) data by ovary weight (g) and preservation method for albacore collected in North Pacific. n = number of fish in sample.

		Mean oocyte diameter (mm)				
		Formalin		Frozen		Percent difference
Ovary weight (g)	n	$\bar{x}$ +/-SE	Range	$\bar{x}$ +/- SE	Range	(formalin vs. frozen)
10–19	19	0.10 ± 0.004	0.07–0.14	0.09 ± 0.003	0.07–0.11	10.0
20–29	27	0.11 ± 0.002	0.09–0.13	0.10 ± 0.002	0.08–0.13	9.1
30–39	11	0.11 ± 0.004	0.08–0.13	0.09 ± 0.032	0.08–0.12	18.1
40–49	2	0.11 ± 0.000	0.11–0.11	0.11 ± 0.002	0.10–0.11	0.0
>50	1	0.11		0.11		0.0
Total	60	0.11 ± 0.002	0.07–0.13	0.10 ± 0.002	0.07–0.13	9.1

significant difference in oocyte diameter (t=0.601, df=225, P>0.05) within method of preservation, and we feel the effects of preservation are largely the source of any differences in measurements.

Ovaries from immature albacore (<88 cm FL) in group C, which had been preserved in 10% formalin, were found to have oocytes in the most developed mode with a significantly larger mean diameter in comparison with those from frozen samples (t=4.614, df=59, P<0.05). The mean diameter of oocytes preserved in 10% buffered formalin was, on average, 9.1% larger than the mean diameter of frozen oocytes (Table 2).

In mature albacore >95 cm FL, the mean diameter of oocytes in the most developed mode within an ovary was measured for each side of the ovary and compared statistically within group B1. Oocytes preserved in 10% buffered formalin were found to have a significantly larger diameter (t=3.581, df=14, P<0.05)—7.1% greater, on average, than the oocyte diameter in frozen ovaries (Table 3).

Thus the mean diameter of oocytes in the most developed mode suggested that mean oocyte diameters of frozen ovaries shrank more than those preserved with 10% formalin. Differential preservation effects were reported by Joseph (1963), who looked at the effects of Gilson's fluid (Simpson, 1951) versus 4% formalin on oocyte diameter in yellowfin and skipjack tuna ovaries. He found that the diameters

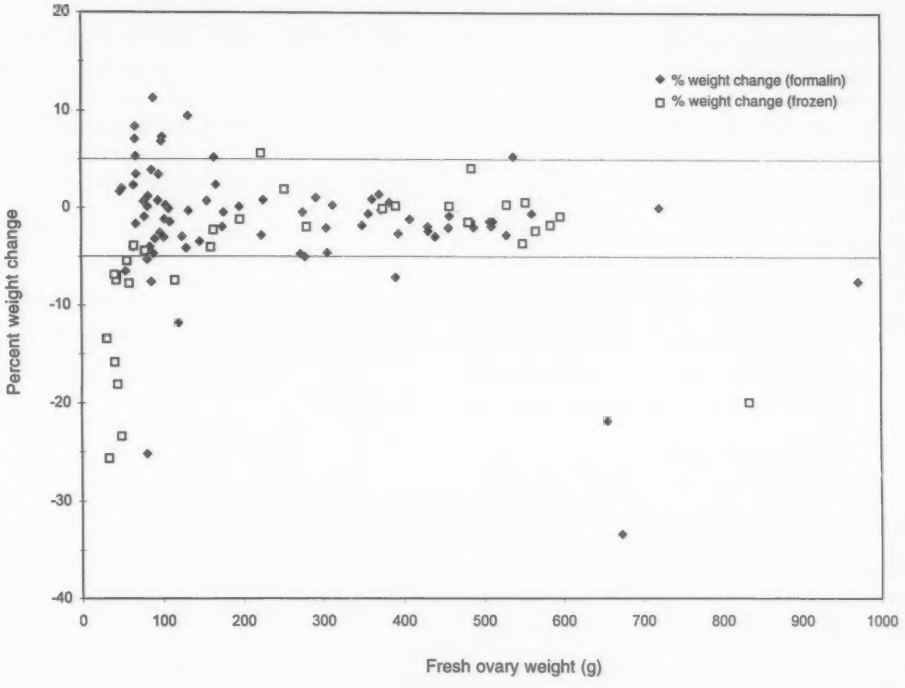

Figure 1

Percent change in ovary weight (fresh versus preserved) for albacore ovaries versus fresh weight in grams for samples collected in Hawaii.

Table 3

Mean oocyte diameter (mm) data by ovary weight (g) and preservation method for albacore collected near Hawaii. n = number of fish in sample.

		Mean oocyte diameter (mm)				
		Formalin		Frozen		
Ovary weight (g)	n	$\bar{x}$ +/-SE	Range	$\bar{x}$ +/- SE	Range	Percent difference (formalin vs. frozen)
<200	11	0.19 ± 0.031	0.12–0.48	0.17 ± 0.027	0.11–0.43	5.3
200–299	1	0.37		0.33		10.8
>300	3	0.59 ± 0.049	0.50–0.67	0.55 ± 0.042	0.48–0.62	6.8
Total	15	0.28 ± 0.049	0.12–0.67	0.26 ± 0.045	0.11–0.62	7.1

of oocytes preserved with Gilson's fluid shrank an average of 24% in comparison with those preserved in 4% formalin. This finding is in contrast with that of Schaefer and Orange (1956) who also examined the effects of Gilson's fluid versus formalin on oocyte diameter. They found that size frequencies for oocytes were similar with both methods for oocytes in the 5–63 μ size range. The strength of formalin used by Schaefer and Orange was greater than that used by Joseph and may be the cause of the different results. Itano[1] examined the effects of brine, refrig-

[1] Itano, D. 1994. Progress report on a large-scale investigation on the reproductive biology of yellowfin tuna in the central and western Pacific region. Fourth meeting of the western Pacific yellowfin tuna research group; Koror, Palau, 9–11 August 1994.

eration, freezing, and 10% formalin on the histological quality of samples of ovary from yellowfin tuna. He reported that histological quality was best for those samples preserved fresh in 10% buffered formalin, whereas samples that had been merely refrigerated could not be used for histology (Itano[1]).

Effect of preservation on weight

The preserved weight of the ovaries from mature fish in group B caught in Hawaii was compared with the fresh weight of ovaries from mature fish in group B (t=2.565, df=94 and P<0.05) and found to have significantly different means at the 95% confidence level. Preserved ovaries averaged a loss of 2% of their fresh weight. Our observations ranged from a loss of 33% to a gain of 11%.

Samples that were frozen (n=31) lost, on average, 6% of their weight and ranged from a loss of 26% to a gain of 6% (Fig. 1). In comparison, those that were preserved in 10% buffered formalin lost, on average, 1% of their weight and ranged from a loss of 33% to a gain of 11%. The greatest difference in albacore ovary weight was observed for ovaries weighing less than 200 g and which had been frozen, as well as for those greater than 600 g and which had been frozen (Fig. 1). The greater percent weight change observed in the smaller ovaries may be a result of processing method. The percentage of weight change for samples greater than 200 g, but less than 600 g, was within 5%. Of the limited number of samples (n=5) greater than 600 g, three of the ovaries that displayed a large loss of weight had oocytes that were hydrating and had mean oocyte diameters near 1 mm.

Conclusion

Freezing was found to have a greater effect on ovarian weight and oocyte diameter than 10% buffered formalin. Consequently, the different methods of preservation used in comparative studies should be evaluated cautiously. Furthermore, a single method of preservation or protocol should be used in a given study.

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Short-term retention of coded wire and internal anchor tags in juvenile common snook, *Centropomus undecimalis*

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Short-term retention rates of coded wire tags and internal anchor-external streamer tags with disk- or T-style anchors was evaluated in snook 110–180 mm SL for 30 days after tagging. The major differences between the two types of internal anchor tags were the shape of the anchor and the size of incision needed to apply the tags, either of which could affect retention or mortality. This study provides baseline information on tag retention rates in common snook that can be used to interpret catch records correctly and to evaluate common snook stocking programs.

Common snook, *Centropomus undecimalis*, are popular gamefish in southern Florida (Bruger and Haddad, 1986) and throughout their range in the southeastern United States and Central America. Snook populations in Florida declined during the 1970's and 1980's despite increasingly strict limits on the fishery (Taylor[1]). In an effort to enhance snook populations, the Florida Department of Environmental Protection has considered developing a stocking program to supplement depleted wild snook stocks. To evaluate a stocking program's success or impact on native populations, hatchery-released fish must be marked to distinguish them from wild fish. Mark retention rates must be known to correctly interpret catch records and to make inferences about the stocking program or the wild population (Wallin and Van Den Avyle, 1994).

Coded wire tags (CWT's) are common in fish stocking programs because they can be applied quickly and economically to small, juvenile fish (<100 mm standard length, SL). Although retention rates of CWT's vary considerably among different species because of morphological differences (Heidinger and Cook, 1988; Szedlmayer and Howe, 1995), retention rates are generally very good (>95%) if appropriate tagging tissues are identified and used (Dunning et al., 1990; Pitman and Isaac, 1995).

A disadvantage with using CWT's is that they cannot be detected by recreational or commercial fishermen; therefore, recovery of CWT data must be obtained independently. Internal anchor-external streamer tags with imprinted information allow recapture information to be obtained from recreational or commercial fisheries. However, these tags are generally restricted for use on fish >110 mm SL. As with CWT's, retention rates of these tags may vary because of morphological differences (Vogelbein and Overstreet, 1987; Waldman et al. 1990).

In this study, we evaluated retention of CWT's and two types of internal anchor-external streamer tags in age-0 common snook. The fish sizes in this study were similar to sizes that would be produced in a large-scale stocking program. We also evaluated the effects of tagging on growth and mortality. Retention of coded wire tags inserted in the cheek musculature was evaluated in common snook 60–115 mm SL for approximately 60 days after tagging. Retention of internal anchor-external streamer tags with disk- or T-style anchors was evaluated in snook 110–180 mm SL for 30 days after tagging. The major differences between the two types of internal anchor tags were the shape of the anchor and the size of incision needed to apply the tags, either of which could affect retention or mortality. This study provides baseline information on tag retention rates in common snook that can be used to interpret catch records correctly and to evaluate common snook stocking programs.

Methods

Coded wire tag retention

We evaluated retention of CWT's and the effects of tagging on growth and mortality in 60–115 mm SL common snook. Equal numbers of fish were randomly assigned to one of three treatment groups: 1) tagged fish, 2) untagged fish that were handled in the same manner as tagged fish but were not tagged, and 3) control fish that were not tagged or handled. The cheek muscle was chosen for tag implantation because of the high CWT retention rates for this location in red drum and striped bass.

Tagged and untagged snook were anesthetized (100 ppm MS-222) just prior to treatment. One person applied all tags. Tags (1-mm-long, 0.25-mm-diameter) were injected vertically, 2 mm deep into the left adductor mandibularis muscle, posterior to the eye with a Northwest Marine Technology (Shaw Island, WA) Mark IV tagging machine.

[1] Taylor, R. 1997. Florida Marine Res. Inst., Florida Dep. of Environmental Protection, 100 Eighth Ave. SE, St. Petersburg, FL 33701-5095. Personal commun.

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Fishery Bulletin 95:873–878 (1997).

Fish were passed through a quality control device (QCD) to ensure tag presence. Fish in the untagged treatment were handled and passed through a QCD in the same manner as tagged fish but were not impaled on a tagging needle. Tagged and untagged fish were placed in separate 1,300-L tanks. Control fish were transferred directly to a 1,300-L tank with minimal disturbance.

The three tanks were aerated and had sand, diatomaceous earth, ultra-violet light, and biological filters. To prevent fish from jumping out, half of each tank was covered with 5-mm nylon mesh net and the other half was covered with opaque black plastic. Water temperatures averaged 24°C (range: 17–30°C); salinity averaged 26 ppt (range: 22–30 ppt); dissolved oxygen averaged 6.4 ppm (range: 4.0–7.4 ppm), and pH averaged 7.8 (range: 7.7–7.9). Fish were fed baitfish or commercially prepared fish chow daily.

Fish in the tagged treatment were checked for tag retention at 3, 30, and 60 days after tagging. At each tag check, fish were anesthetized (100 ppm MS-222), checked for tag presence with a field sampling detector (Northwest Marine Technology), and measured. Fish in the untagged treatment were similarly anesthetized and measured at 3 and 30 days after tagging. Dead fish were removed from the tanks and checked for tag presence.

We assumed that mortality associated with tagging or handling would occur within 30 days of tagging (Szedlmayer and Howe, 1995). Therefore, after 30 days, fish in the untagged and control groups were combined and then randomly divided into two groups that received either the tagged or untagged treatment. This created a second trial of the experiment to evaluate CWT retention. Fish in the second trial were checked for tag retention at 3 and 30 days after tagging.

The entire experiment was repeated three times with fish from different culture facilities, resulting in three trials in which tag retention was evaluated for 30 days and three trials in which tag retention was evaluated for 30 and 60 days. Mean initial fish sizes varied among trials from 62 to 115 mm SL, and numbers of fish per treatment varied among trials from 24 to 76 (Table 1).

Table 1

Tag (coded wire) retention rates and fish survival rates at 3, 30, and 60 d after tagging for each treatment (tagged fish, untagged fish, and control fish) and fish sizes at the time of tagging. Starting no. = number of fish at the beginning of the experiment. Survival rates are from the start of the experiment until 3, 30, or 60 d after tagging. Standard length at the time of tagging is given as the mean with standard deviation in parentheses.

Trial	Treatment	Starting no.	Standard length (mm)	Tag retention rates (%)			Survival rates (%)		
				3-day	30-day	60-day	3-day	30-day	60-day
1	Tagged	26	92 (6.8)	100	100	100	100	92.3	92.3
	Untagged	24	95 (5.9)	—	—	—	92.3	92.3	—
	Control	26	94 (6.4)	—	—	—	100	100	—
2	Tagged	24	115 (9.7)	100	100	—	100	95.8	—
	Untagged	24	117 (9.6)	—	—	—	100	100	—
3	Tagged	76	62 (8.3)	98.6	92.0	85.4	98.7	67.1	63.1
	Untagged	76	59 (8.3)	—	—	—	100	93.1	—
	Control	75	59 (8.2)	—	—	—	100	81.3	—
4	Tagged	62	63 (9.2)	100	87.1	—	100	100	—
	Untagged	61	63 (9.2)	—	—	—	100	100	—
5	Tagged	74	74 (7.8)	100	95.8	95.8	98.6	98.6	98.6
	Untagged	75	71 (8.4)	—	—	—	98.7	98.7	—
	Control	75	75 (8.7)	—	—	—	100	100	—
6	Tagged	74	82 (10.1)	100	98.6	—	100	97.3	—
	Untagged	75	81 (9.4)	—	—	—	100	100	—
Overall	Tagged	—	71 (14.5)	99.8	95.6	93.7	99.6	91.9	84.7
	Untagged	—	73 (16.6)	—	—	—	98.5	97.4	—
	Control	—	72 (17.3)	—	—	—	100	93.8	—

Retention of internal anchor tags with external streamers

We evaluated retention of internal anchor tags with external streamers (disk and T-style) in 110–180 mm SL common snook. Tags with disk anchors (Model FM-89SL, Floy Mfg., Seattle, WA) consisted of a plastic 5 × 15 mm imprinted elliptical disk and 50-mm imprinted streamer. T-anchor tags (IEX tags, Hallprint Ltd., Holden Hill, Australia) consisted of an 18-mm T-shaped anchor and a 42-mm imprinted streamer. Equal numbers of fish were randomly assigned to one of three treatments: 1) fish tagged with disk anchor tags, 2) fish tagged with T-anchor tags, and 3) untagged fish that were handled in the same manner as tagged fish.

All fish were anesthetized (100 ppm MS-222) and measured just prior to treatment. To apply disk anchor tags, we used a scalpel to make an approximately 6-mm vertical incision into the body wall and then inserted the disk into the incision. To apply the T-anchor tags, we used a sharpened tag-applicator needle to make an approximately 2-mm diameter puncture and then inserted the T-anchor into the opening. Incisions were made on the left ventral side of the fish, anterior to the vent and posterior to the pectoral fin. Anchors were dipped in betadyne prior to insertion to minimize infection. Fish in the tag treatments were distinguished by fin clips: disk anchor-tagged fish received a left pectoral fin clip and T-anchor-tagged fish received a right pectoral fin clip. Fish in the untagged treatment were anesthetized, measured, and handled in the same manner as tagged fish but did not receive an incision or finclip. All fish were transferred immediately after treatment to a 13,300-L tank containing approximately 9,000 L of water. The tank was aerated and had sand, diatomateous earth, and biological filters. Water temperatures averaged 27°C (range: 24–29°C); salinity averaged 26 ppt (range: 11–30 ppt); dissolved oxygen averaged 6.5 ppm (range: 4.9–8.4 ppm), and pH averaged 7.8 (range: 7.7–7.9 ppm). Fish were fed live baitfish daily.

Fish were checked for tag retention at 14 and 30 days after tagging. At each tag check, fish were anesthetized (100 ppm MS-222), checked for tag and finclip presence, measured, and weighed. The entire experiment was repeated twice; numbers of fish per treatment varied between trials from 61 to 78 fish per treatment (Table 1). During the first trial, necropsies were performed on three to ten fish from each treatment after 14 days to evaluate a bacterial infection. Six of ten T-anchor-tagged fish examined had anchors that were inserted into the swim bladder, whereas all disk-anchor-tagged fish examined (n=3) had anchors that were correctly placed in the peritoneal cavity. Because of the potential for misapplication with the T-anchor tag, during the second trial we applied T-anchor tags by making a 3-mm scalpel incision rather than by making a puncture with a tag applicator needle. At the end of the second trial, ten randomly selected fish from each tag treatment were dissected and examined for tag implant locations and tissue healing.

Analyses

Estimates of the rates of tag retention and survival were arcsine-transformed prior to analysis (Sokal and Rohlf, 1981). Fish size at the time of tagging differed significantly among trials in both the CWT experiments (ANOVA, df=5, F=517.6, P<0.01) and in the internal-anchor-tag experiments (ANOVA, df=1, F=6.7, P<0.01). Therefore, mean size at tagging was used as a covariate in analysis of covariance (Sokal and Rohlf, 1981; SAS, 1989) to compare rates of tag retention, survival, and growth among time periods and treatment groups. Post hoc comparisons were conducted with the method of least-square means (SAS Institute, Inc., 1989).

Results

Overall, retention rates of coded wire tags averaged 99.8%, 95.6%, and 93.7% at 3, 30, and 60 days after tagging, respectively (Table 1). At 3 days, tag retention rates for all sizes of snook ranged from 98.6 to 100% (Fig. 1). Fish size at the time of tagging significantly affected tag retention rates (F=12.5, P<0.01); larger fish had higher retention rates, particularly during the 30- to 60-d period after tagging (Fig. 1). Tag retention of common snook >70 mm SL at the time of tagging was ≥95% at 30 and 60 days after tagging, whereas tag retention in snook <65 mm SL was 92.0% and 85.4% at 30–60 days after tagging, respectively (Table 1; Fig. 1). Tag retention rates decreased between 3 and 30 days after tagging (LSMEANS, P=0.02) but did not change significantly between 30 and 60 days (LSMEANS, P=0.89; Fig. 2).

Survival rates of CWT fish were not significantly different from those of the untagged or control fish (df=2, F=0.5, P=0.61). Survival rates of fish in all treatments averaged 99.6%, 91.9%, and 84.7% at 3, 30, and 60 days after tagging, respectively (Table 1). Poor survival of fish in the third trial (63%, Table 1) is attributed to parasitic infection. Growth rates of CWT fish were also not significantly different from those of untagged or control fish (df=2, F=0.87, P=0.42).

Overall, retention rates of T-anchor and disk-anchor tags averaged 100% and 99.2%, respectively, after 30 days (Table 2). Fish size at the time of tagging did not significantly affect internal anchor tag retention rates (df=1, F=0.3, P=0.64). Retention rates did not differ significantly between disk- and T-anchor–tagged fish or among time periods (for both comparisons, df=1, F=0.8, P=0.43). There were also no significant differences in survival (df=2, F=0.7, P=0.55) or growth (df=2, F=0.03, P=0.10) among treatments . Survival rates of T-anchor- and disk-anchor–tagged fish averaged 97.0 and 91.9% at 14 and 30 days after tagging, respectively (Table 2).

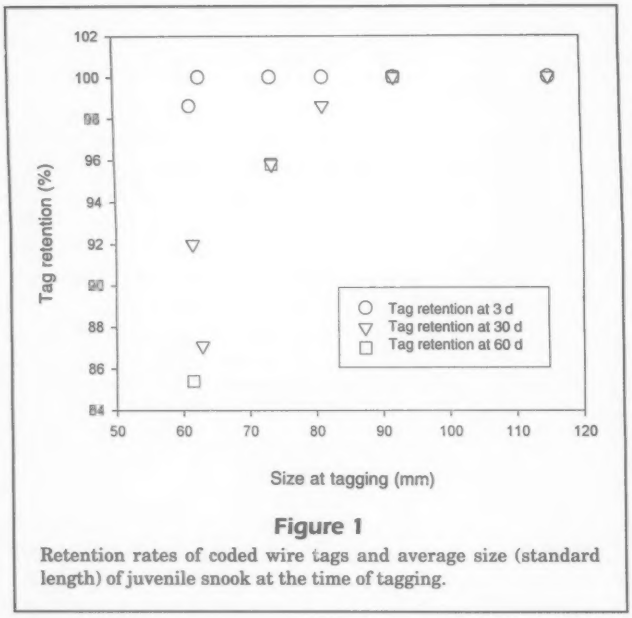

Figure 1

Retention rates of coded wire tags and average size (standard length) of juvenile snook at the time of tagging.

Nearly all (80%) fish with internal anchor tags examined at 30 days had inflammation or a proliferation of epithelial cells at the tag insertion site. Of the ten disk-tagged fish examined after the second trial, six fish had anchors encapsulated in the peritoneum, two fish had anchors inserted in the swim bladder or gastrointestinal tract, and two fish had anchors freely moving in the peritoneal cavity. Of the ten T-anchor–tagged fish examined, two fish had anchors encapsulated in the peritoneum, one had an anchor inserted in the swim bladder, and seven had anchors that were freely moving in the peritoneal cavity.

Discussion

The high retention rates of CWT's reported in this study (85–100%) indicate that CWT's are effective for marking age-0 common snook and that the cheek musculature is appropriate for tagging. CWT's did not affect snook survival or growth during the first 30–60 days after tagging, indicating that CWT's have negligible adverse effects during this time period. CWT retention rates increased with initial fish size (Fig. 1) from 87–92% for snook with an initial mean size of 62 mm SL to 95–100% for snook with initial mean sizes of 71–117 mm SL. Several authors have noted the importance of fish size or target tissue size in the retention of CWT's (Heidinger and Cook, 1988; Szedlmayer and Howe, 1995). Our study also shows a relation between initial tagging size and CWT retention.

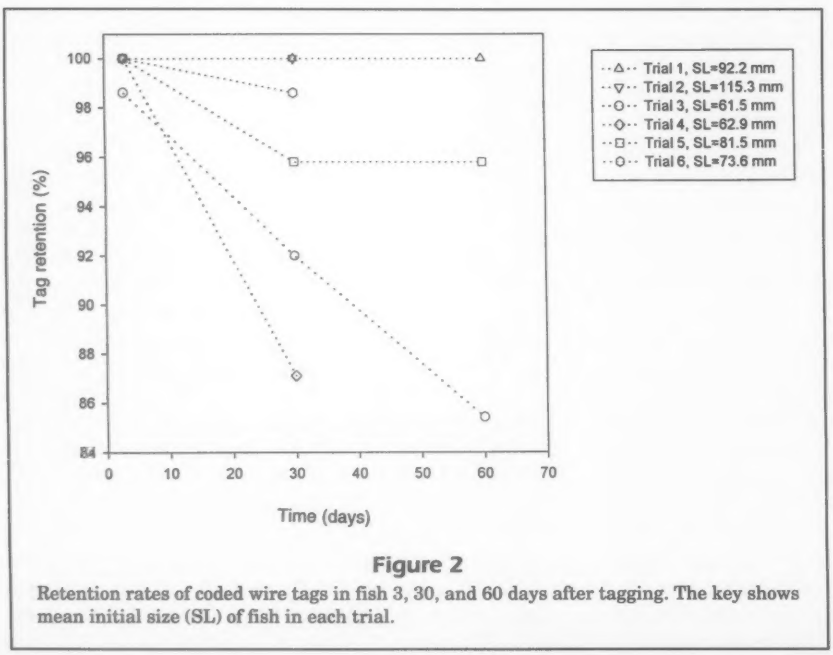

Figure 2

Retention rates of coded wire tags in fish 3, 30, and 60 days after tagging. The key shows mean initial size (SL) of fish in each trial.

Most tag loss occurred between 3 and 30 days (Fig. 2). Other studies have noted

Table 2

Internal anchor tag retention rates and fish survival rates at 14 and 30 d after tagging for each treatment (t-bar–tagged fish, disk-tagged fish, and control fish) and fish sizes at the time of tagging. Starting no. = number of fish at the beginning of the experiment. Survival rates are from the start of the experiment until 14 or 30 d after tagging. Standard length at the time of tagging is given as the mean with standard deviation in parentheses.

Trial	Treatment	Starting no.	Standard length (mm)	Tag retention rates (%)		Survival rates (%)	
				14-day	30-day	14-day	30-day
1	T-bar–tagged	78	139 (13.1)	100	100	93.6	93.6
	Disk-tagged	78	138 (13.0)	100	100	91.0	75.6
	Control	78	137 (13.7)	—	—	97.4	82.1
2	T-bar–tagged	61	135 (11.3)	100	100	100	100
	Disk-tagged	61	136 (10.4)	100	98.4	100	100
	Control	61	134 (10.7)	—	—	100	100
Overall	T-bar–tagged	—	136 (12.5)	100	100	96.8	96.8
	Disk-tagged	—	137 (11.9)	100	99.2	95.5	87.8
	Control	—	137 (12.6)	—	—	98.7	91.1

that most CWT loss in juvenile fish occurs within two to four weeks after tagging, the time period corresponding with the time required for the tagging puncture wound to heal (Dunning et al., 1990). Although there was no significant change in retention rates after 30 days, tag retention rates in the smallest fish (mean SL 62 mm) continued to decline between 30 and 60 days (Fig. 2), providing further evidence of the importance of fish size for tag retention.

Thirty-day retention rates of both types of internal anchor-external streamer tags were very high (>99%), indicating that these tag types are effective tools for marking >110 mm common snook. However, other studies have suggested that retention of disk- and T-anchor tags may decrease over months or years and should therefore be evaluated for longer periods of time (Collins et al., 1994). Although the incisions required to apply disk tags are larger than incisions required for T-anchor tags, there was no difference in survival or growth rates of fish with either tag type. Both tag types caused similar incidences of irritation at the tag insertion site. Similar irritation has been noted in other fish species and can eventually result in tag loss (Mattson et al., 1990; Collins et al., 1994). After 30 days, disk anchors were more frequently encapsulated and attached to the inside of the body wall than were T-anchors. Both tag types were equally likely to be incorrectly inserted in the swim bladder or gastrointestinal tract when the incision was made with a scalpel; overall, incorrect insertions were noted in 10–20% of the fish examined. We recommend using scalpels to insert the T-anchor tags; when a tag applicator needle was used, incidences of incorrect insertion increased to 60%, probably because of difficulty in controlling puncture depth.

In conclusion, because CWT retention rates were significantly improved for fish >70 mm SL, we recommend tagging snook at this size whenever possible. We also recommend that CWT retention in snook be evaluated for 30 days after tagging so that accurate estimates of tag-loss rates can be calculated. For snook >110 mm SL, both the T-anchor and disk internal anchor-external streamer tags were effective marking techniques. For all types of tags and all sizes of fish in our study, tagging did not significantly affect snook survival or growth.

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Fishery Bulletin

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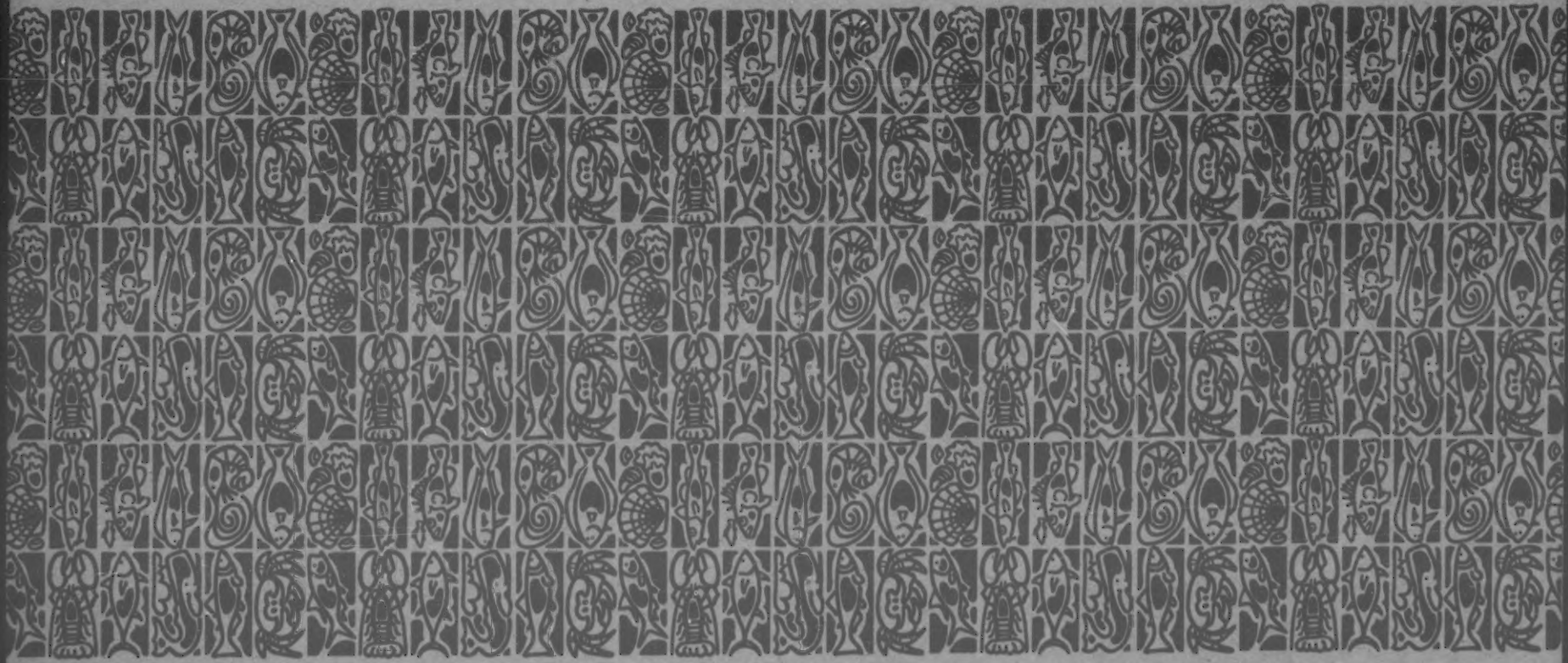

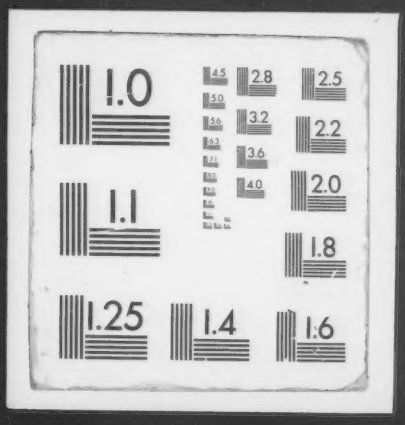
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